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: Current status, future challenges, and biotechnological
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2020-11

Ramakrishnan , M , Yrjälä , K , Vinod , K K , Sharma , A , Cho , J , Satheesh , V & Zhou , M
2020 , ' Genetics and genomics of moso bamboo (*Phyllostachys edulis*) : Current status,
future challenges, and biotechnological opportunities toward a sustainable bamboo industry '
, Food and Energy Security , vol. 9 , no. 4 , 229 . <https://doi.org/10.1002/fes3.229>

<http://hdl.handle.net/10138/327079>

<https://doi.org/10.1002/fes3.229>

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REVIEW



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Genetics and genomics of moso bamboo (*Phyllostachys edulis*): Current status, future challenges, and biotechnological opportunities toward a sustainable bamboo industry

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Funding information

National Natural Science Foundation of China, Grant/Award Number: 31870656 and 31470615; Zhejiang Provincial Natural Science Foundation of China, Grant/Award Number: LZ19C160001

Abstract

Sustainable goals for contemporary world seek viable solutions for interconnected challenges, particularly in the fields of food and energy security and climate change. We present bamboo, one of the versatile plant species on earth, as an ideal candidate for bioeconomy for meeting some of these challenges. With its potential realized, particularly in the industrial sector, countries such as China are going extensive with bamboo development and cultivation to support a myriad of industrial uses. These include timber, fiber, biofuel, paper, food, and medicinal industries. Bamboo is an ecologically viable choice, having better adaptation to wider environments than do other grasses, and can help to restore degraded lands and mitigate climate change. Bamboo, as a crop species, has not become amenable to genetic improvement, due to its long breeding cycle, perennial nature, and monocarpic behavior. One of the commonly used species, moso bamboo (*Phyllostachys edulis*) is a potential candidate that qualifies as industrial bamboo. With its whole-genome information released, genetic manipulations of moso bamboo offer tremendous potential to meet the industrial expectations either in quality or in quantity. Further, bamboo cultivation can expect several natural hindrances through biotic and abiotic stresses, which needs viable solutions such as genetic resistance. Taking a pragmatic view of these future requirements, we have compiled the present status of bamboo physiology, genetics, genomics, and biotechnology, particularly of moso bamboo, to drive various implications

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in meeting industrial and cultivation requirements. We also discuss challenges underway, caveats, and contextual opportunities concerning sustainable development.

KEYWORDS

bamboo industry, bioeconomy, biotechnology, genomics, moso bamboo, *Phyllostachys edulis*, sustainable development, transposons

1 | INTRODUCTION

Three formidable interlinked challenges of the contemporary world, solutions for which articulate a sustainable future, are food security, energy security, and climate change (Karp & Richter, 2011; Lal, 2010). Among the several solutions to meet the conglomerated challenges, bamboo stays ahead as one of the plant species that can sustain the future world through its versatile nature (Ramakrishnan, Zhou, Baskar, & Packiam, 2018). Bamboo, the prime member of the largest grass family, Poaceae, belongs to the subfamily Bambusoideae consisting of 75 genera accommodating 1,642 bamboo species (Vorontsova, Clark, Dransfield, Govaerts, & Baker, 2016). It is the only grass that grows in a wide range of climates and widely distributed across the Asia Pacific, Americas, and Africa (Figure 1). Among different bamboos, woody bamboos, both tropical and temperate, are most commercially used for numerous uses (Figure S1) such as renewable energy resources (biofuels and charcoals), timber, raw materials for craft and various household products, materials for house building and furnishing, and also as food resource and medicines (Li, Wei, Xu, Xu, & He, 2018; Panee, 2015; Song et al., 2016; Vogtlander & Van der Lugt, 2014; Wróblewska, De Oliveira, Grombone-Guaratini, & Moreno, 2018; Yuan, Wang, Pan, Shen, & Wu, 2019; Zhaohua & Wei, 2018). It can also be used to conserve rainforests saving both the natural diversity and paper and pulp industry (Chen, Li, et al., 2019; Jiang, 2007), and it significantly contributes to carbon sequestration (Li et al., 2015; Wu et al., 2019; Xu, Ji, &

Zhuang, 2018; Xu et al., 2011). Bamboo biomass increases at a rate of 10%–30% annually, as against 2%–5% growth of other timber species (Atanda, 2015). Bamboos, owing to the faster growth, can easily be harvested within 4–5 years, unlike that of most softwoods, which take 15–20 years. Thus, annual international trade of bamboo stands more than \$2.5 billion (<https://www.inbar.int>) (Wang, Sun, Ding, et al., 2019; Zhao et al., 2017). So, we, in this review, attempt to take a comprehensive view of how biotechnology, particularly in areas of molecular genetics, genomics, and quantitative genetics, can play a decisive role in the development of bamboo for industries.

1.1 | Industrial relevance of moso bamboo

Belonging to the tribe Arundinarieae, moso bamboo (*Phyllostachys edulis* (Carrière) J. Houz) is a major species of woody bamboo cultivated in South Asia, Africa, and America (Clark, Londoño, & Ruiz-Sanchez, 2015; Wang, Chen, Liu, & Liu, 2020). It lives for about 60 or more years and is widely adapted and amenable to different cultivation systems from agroforestry and monoculture gardens. Being one of the fastest-growing bamboos (Wei et al., 2018), moso bamboo has a unique rhizome-dependent proliferation system (Li, Li, Lu, & Chen, 2019; Tao, Fu, & Zhou, 2018; Wei et al., 2019) that runs radially from the mother plant. The rhizomes are thick and segmented and remain underground at shallow depths of about 50 cm. Depending on the length,

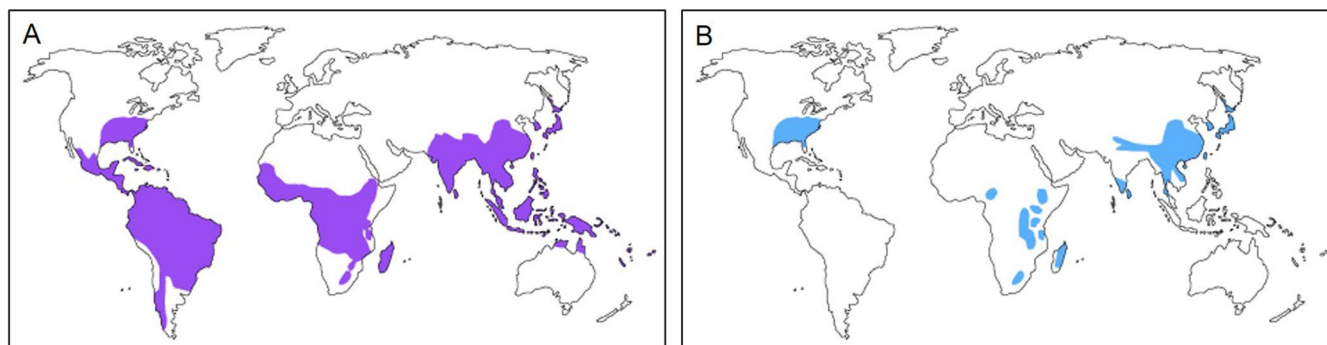


FIGURE 1 Universal distribution of bamboo species (Bambuseae) from sea level to snow line. A. distribution of all woody bamboo represented in purple; B. distribution of temperate woody bamboos is indicated by light blue.

Source: <https://www.eeob.iastate.edu/research/bamboo/maps.html>

a single rhizome can have up to a hundred buds at nodes. Under conducive conditions, bud burst occurs, and the emerging culms grow very fast. Shoots can reach up to 50 m in height, growing at a rate of about one meter per day during the peak growth phase, and can continue to increase in girth and thickness. A grown-up culm can have a diameter of about 20 cm, and with very high mechanical strength (Wang, Sun, Xu, Yang, Zhao, et al., 2019). These extraordinary properties of the culms qualify moso bamboo as an industrial bamboo, earning the name “giant” or “timber” bamboo. Focused research is on understanding the molecular mechanisms of moso bamboo growth (Singh et al., 2013).

In the United States, moso bamboo is commercially grown by several industries for biochar, biofuel, and structural bamboo products (David et al., 2019). Similarly, the commercial viability of moso bamboo has resulted in widespread cultivation in Asian countries (Jiang et al., 2017). In China, it occupies about 4.43 million ha covering about 73.8% of the bamboo-growing area (Jiang, 2007). Most of the industrial relevance of moso bamboo arises out of its exceptional wood quality, which is used to develop engineered structural bamboo products that are used as a substitute for engineered wood products such as plywood and laminated timber. The flexural and compressive properties show that the bamboo wood is as good as most of the commercial timber woods (Dixon & Gibson, 2014).

In the bamboo literature, many good reviews are available on the efficient utilization and practical applications of bamboo (He et al., 2014; Liese, Welling, & Tang, 2015). But only a few exist on biotechnological applications for bamboo improvement, particularly related to industrial use, mainly focusing on sustainable bamboo development in a wider context of bioeconomy and circular economy. Mudoi et al. (2013) focused on the progress in micropropagation of important bamboos. Singh et al. (2013) reviewed the limitations, progress, and prospects of the application of biotechnological tools in bamboo improvement, providing an overview of molecular marker systems and their prospective use. In their review on advances in bamboo molecular biology, Jiang and Zhou (2014) underpinned the need for extensive bamboo phylogenetic analysis and the use of genomic information and tools for bamboo breeding. Further, Yeasmin, Ali, Gantait, and Chakraborty (2015) overviewed the genetic diversity and characterization on bamboos, while extensive coverage on the in vitro flowering of woody bamboo has been presented by Yuan, Yue, Gu, and Lin (2017) and Sandhu, Wani, and Jiménez (2018).

In this review, we attempt to highlight the potential for bamboo development, more specifically of moso bamboo, through genomics-assisted breeding, extensively covering physiology, genetics, genomics, and biotechnology. We discuss the outcomes of genomic studies on transcriptomic and proteomic aspects of moso bamboo growth, flowering, stress

responses, and transposon diversity to address prospects for future sustainable development. We hypothesize that biotechnology has a lot more things to offer into the transformation of moso bamboo as an ideal candidate crop for bioeconomy. China has a lead role to play in bamboo development as the first country in the world, which adopted a law for the circular economy in 2008 (CIRAIG, 2015), a potential already recognized by the European Union, for creating sustainable annual gains from the manufacturing sector.

2 | GENETICS AND GENOMICS OF MOSO BAMBOO

2.1 | Evolution and diversity

Bamboo has been identified as an important plant that leads to shape human civilizations, particularly in the south and Southeast Asia. Tracing the genetic history of bamboos by paleogeographic studies on bamboo leaves and pollen reveals diversification of bamboo in the late Miocene at Zhejiang Province, which resulted in the wide distribution of bamboos in southern China (Wang, Ma, et al., 2014). Plastid genome-based phylogenetic evaluation of bamboos identifies four major lineages, herbaceous, temperate, neotropical, and paleotropical (Kelchner, 2013), among which the temperate woody group is the largest among the bamboos, and was identified as genetically very distinct. The moso bamboo belongs to this group. Other distinct clades identified in this study include herbaceous clade belonging to the tribe Olyreae (Bouchenak-Khelladi et al., 2008), while the remaining tropical woody and neotropical woody (tribe Bambuseae) show less distinct patterning. Further, Peng, Lu, et al., 2013, while presenting the draft genome of moso bamboo, reported the genetic closeness of bamboo with that of other C3 grasses, especially belonging to the BEP clade consisting of subfamilies Bambusoideae, Ehrhartoideae (formerly Oryzoideae), and Pooideae. Although plastid genome diversity could divulge the evolutionary pattern, it could not resolve with certainty the relationship among clades other than that of temperate woody bamboos. Recent advancements in genomics can now give the taxonomy a firmer basis. The latest release of five draft bamboo genomes belonging to paleotropical (*Bonia amplexicaulis*), neotropical (*Guadua angustifolia*), and herbaceous (*Olyra latifolia*, *Raddia guianensis*, and *R. distichophylla*) clades provides further insights into bamboo evolution (Guo, Ma, et al., 2019; Li, Shi, et al., 2020). These genomes represented three ploidy levels—diploid, tetraploid, and hexaploid—with different geographical origins. The study of the first high-density linkage map of the hexaploid woody bamboo revealed that it evolved after herbaceous bamboos had diverged through three independent allopolyploid events (Guo, Ma, et al., 2019). Further, analysis

of the model genomes has led to the understanding that over 90% of the bamboo protein-coding genes had conserved functional domains, leading to the constructing a reticulate evolutionary model for Bambusoideae subfamily.

Indicating its evolutionary significance, moso bamboo has been reported to have significant levels of natural genetic diversity (Gui et al., 2007; Kumar, Turner, Rao, & Arumuganathan, 2011; Zhao, Zhang, et al., 2013), with its genome diversified earlier than 65 million years ago (Peng, Lu, et al., 2013). Native to mainland China and naturalized in other parts of the world, the syntenic genomic relationship of moso bamboo with rice and sorghum has also been reported earlier (Gui et al., 2010; Peng, Lu, et al., 2013). In one of the studies, the AP2/ERF (APETALA2/ethylene-responsive factor) transcription factor (TF) in moso bamboo was found diversified from rice AP2/ERF genes 15–23 million years ago (Wu, Lv, et al., 2015). This indicates that bamboos have a long evolutionary history than most of the cultivated cereals. A phylogenetic tree constructed based on single-copy orthologous genes showed that the moso bamboo had close proximity with purple false brome, rice, and sorghum. Among the bamboos, moso bamboo was recognized as a tetraploid (Friar & Kochert, 1991) having 48 chromosomes ($2n = 48$). Supporting this view, the presence of high number of clustered gene families in the draft genome assembly pointed toward a putative whole-genome duplication that occurred 7–12 million years ago (Peng, Lu, et al., 2013). Later, the chromosome-level reference genome that covered 95% of the genomic region reinforced the theory of whole-genome duplication, thereby identifying moso bamboo as a tetraploid having evolved from a diploid ancestor (Guo, Ma, et al., 2019; Zhao, Gao, et al., 2018). Moso bamboo is identified to have a neutral karyotype symmetry (Zhou, Xu, Shen, Xiang, & Tang, 2017), with a genome size of about 2,000 Mb (Gui et al., 2007; Zhao, Gao, et al., 2018).

During the evolutionary process, whole-genome duplication has helped the bamboo genome to acquire adaptive abilities. Whole-genome duplication leads to development of multigene superfamilies, the family of genes that share considerable homology with the common ancestor. They are historically related but functionally diverged group of genes that may have undergone both structural divergence and positional divergence across the genomes (Hartl & Clark, 2007). One of the characteristics of the multigene superfamilies is the modular gene expression, a process called exon duplication and shuffling. Exon shuffling favors stitching up of different modules of the functional genes that comes from different parts of the genome to create variation in the functional proteins that aid in the adaptive process (Kolkman & Stemmer, 2001; Long, Betrán, Thornton, & Wang, 2003). This is facilitated through a process called alternative splicing (AS), a process that helps higher genomes to shuffle

exons (Liu & Grigoriev, 2004). Li, Shi, et al. (2018), in a recent study using moso bamboo, showed how AS influenced bamboo evolution, wherein they reported different splicing events differed in different tissues and are adjusted to different growth stages. Rhizome and fast-growing shoot tissues showed more AS events, and approximately 60% of genes were alternatively spliced in fast-growing shoots, the winter bamboo shoot having shown the highest number of AS events. Further, they observed that highly conserved genes had more AS events. AS is regarded as the main factor responsible for the bamboo shoot and flowering gene diversity, as well as for developing genes for drought response.

2.2 | Classical genetics and breeding

Compared with other plant species, extensive genetic studies on biology and breeding in bamboo remain limited. There are only a few traits that have been studied, and information on their genetic control remains largely obscure. A major impediment in such investigations is the long flowering cycle and huge resources and time required to handle populations or germplasm because they are short-lived and in a chaotic status in different places of the world (Hui, Liang, Yang, & Chen, 2014). Bamboo is agronomically difficult to improve by selective breeding. Although the bamboo breeders have been working tirelessly on several challenges of crop improvement, the progress from conventional breeding attempts has been extremely slow. Singh et al. (2013) concluded that it is equally difficult to develop hybrid bamboo to exploit heterosis using traditional breeding approaches. Therefore, current genetic information in bamboos is limited to trait variability, diversity, and taxonomic classification on the basis of morphological characters. Yeasmin et al. (2015) pointed out that classification based on morphological characters is not very reliable since they are often influenced by ecological and environmental factors. Hardly, any information is available on the interclonal hybridization of bamboo, but an attempt to produce intergeneric crosses between bamboo and sugarcane has been reported from India (Rao, Alexander, & Kandasami, 1967, 1969). Although embryo rescue has been tried to recover *Bambusa* × *Saccharum* hybrid, the attempt remained mostly unsuccessful.

2.3 | Genetic resources

Unlike other domesticated crop species, bamboos remain almost wild in their genetic makeup even when grown under conservation in bambusetta worldwide. In several parts of the world, such bambusetta comprise of either ornamental bamboos for aesthetic purposes. However, utility bamboos

are grown around households for the specific purpose of domestic uses such as poles, ladders, and raw materials for handicrafts, furniture, and utensils. Generally, these bamboos remain largely uncharacterized and unutilized in breeding programs. On the other hand, large woody bamboos such as moso bamboo are conserved in their natural habitats in countries such as China. These nature reserves occupy large areas for meeting the local requirements. Nature reserves maintained at China's Yunnan province has a total of 108 groves, of which five are recognized as of national importance (Hui, 1999; Hui et al., 2014).

Despite of its recognition as an important plant species, organized germplasm collection and conservation in bamboos remain limited. Notwithstanding, several botanical collections of bamboo do exist around the world, particularly in botanical gardens in countries such as Sri Lanka, Indonesia, China, Japan, Bangladesh, and India. China has more than 20 botanical gardens wherein bamboos are conserved (Fu, 1999), the largest collection being the bamboo garden at South China Botanical Garden in Guangzhou comprising of more than 200 species (Huang, 2010). While 136 species, subspecies, and varieties are conserved at Xishuangbanna Tropical Botanical Garden at Yunnan, Hangzhou Botanical Garden in Zhejiang Province conserves 100 species of bamboo belonging to 16 genera and 74 bamboo species are conserved in Shanghai Botanical Garden in Shanghai. Except China and few collections in India, organized bamboo conservation has not been a practice around the world, to aid bamboo improvement. Toward meeting this, under the aegis of INBAR and Biodiversity International (then International Plant Genetic Resources Institute), a training program was organized at Yunnan, China, on bamboo germplasm conservation, diversity, ecogeography, resource utilization, and taxonomy (Rao & Rao, 1999). In this program, guidelines for bamboo collection and documentation were released (Kochhar, 1999).

As the most prominent commercial species, moso bamboo enjoys 61% of cultivation extent in China. Still, moso bamboo does not have a specialized germplasm conservation center so far. The major reason is the complexity in its propagation pattern, which is often through rhizomes than by seeds. This hinders live conservation of propagules by storage, which require large facilities and wide area for ex situ conservation. Further, moso bamboo grows naturally in three provinces of China (Zhejiang, Fujian, and Sichuan), and not in other parts. Because of the long breeding cycle, moso bamboo seeds from genetic variants located at different places are not available regularly, making the conservation effort chaotic. Furthermore, the seed viability is very limited and does not go beyond 2 years under storage. Being introduced from China, germplasm repositories of moso bamboo in other nations such as India, Japan, Korea, Myanmar, and Australia seldom exist.

3 | ROLE OF NEXT-GENERATION SEQUENCING APPROACHES IN EXPEDITING THE CROP IMPROVEMENT

3.1 | The current status of the bamboo genome information

The contemporary developments in whole-genome sequencing and analytical methodologies have upscaled the understanding of whole genomes of several plants (Bolger et al., 2014). Currently, complete genome sequence of many plant species, particularly of the major crops belonging to Poaceae grass family, is available to plant breeders for integrating into crop improvement (<https://phytozome-next.jgi.doe.gov/>). Following the advancements in other crops, in 2017, the International Network for Bamboo and Rattan (www.inbar.int) launched a mega project called “Genome Atlas of Bamboo and Rattan (GABR)” to elucidate bamboo and rattan (BR) genetics toward development into a bioeconomy. Besides several other subprojects, GABR includes two core subprojects, Bamboo-T1K (Transcriptomes of 1,000 bamboos) and Rattan-G5 (genomes of five Rattans) (Zhao et al., 2017). Under this program, in 2018, chromosome-level assemblies of moso bamboo (Zhao, Gao, et al., 2018) and two rattan species (Zhao, Wang, et al., 2018) were released.

Genome-level explorations in bamboo were begun in 2010 and 2011, by the release of genome-wide full-length cDNA (Peng et al., 2010) and chloroplast genome sequences (Zhang, Ma, & Li, 2011) of moso bamboo and few allied species. Subsequently, draft genome scaffold of moso bamboo was delivered in 2013 by Peng, Lu, et al. (2013). This was the first release of any genome among the Bambusoideae subfamily, construction of which was based on whole-genome and transcriptome sequences. The draft had a size of 2,050 Mb with 31,987 predicted genes having an average length of 3,350 bp per gene. Advancing further, in 2018, a chromosome-level de novo assembly of moso bamboo genome was released (Zhao, Gao, et al., 2018) that used high-throughput Hi-C scaffolding strategy. This assembly has a significant genome coverage improvement of more than 243 times over the draft genome. The size of the genome was 1,908 Mb with an N50 scaffold length of 79.90 Mb. The genome reference reads contained a total of 51,074 high-quality protein-coding genes. The genome details with the latest annotation are freely available at the GigaScience database (gigadb.org). By size, moso bamboo genome is 7.8 times larger than the smallest known grass genome of the resurrection grass, *Oropetium thomaeum*, which is 245 Mb long (Bartels & Mattar, 2002; VanBuren, Wai, Keilwagen, & Pardo, 2018). Also, it is 4.4 times larger than rice genome (430 Mb, Sasaki, 2005), and 2.5 times bigger than sorghum genome (772 Mb, Paterson et al., 2009). Relatively, moso bamboo genome is smaller

than that of corn (~2,500 Mb, Schnable et al., 2009), hexaploid wheat (17,000 Mb, Brenchley et al., 2012; Consortium IWGS, 2014), and barley (5,300 Mb) (Consortium IBGS, 2012; Linde-Laursen, Heslop-Harrison, Shepherd, & Taketa, 1997).

Being one of the latest genomes to be unraveled (Guo, Ma, et al., 2019; Zhao, Gao, et al., 2018), the high level moso bamboo genome is an important milestone in bamboo research and development. Although not put into extensive usage so far, among the recent genome-based studies, Zhou, Wu, Ramakrishnan, Meng, and Vinod (2018) attempted to unfurl the natural variants of moso bamboo through genome resequencing by identifying several structural and copy-number variations. They drew implications on the prospective use of these variants into bamboo improvement. Additionally, they identified transposon variations that depict adaptive responses during the evolutionary process of moso bamboo. Subsequently, through functional analyses of transposons, Ramakrishnan, Zhou, Pan, Hänninen, Yrjälä, et al. (2019), Ramakrishnan, Zhou, Pan, Hänninen, Tang, et al. (2019) identified activities of mariner-like elements (*MLE*) of the moso bamboo, drawing evolutionary connotations.

3.2 | Genome databases

Based on the draft genome, Zhao et al. (2014) established the first bamboo genome database (BambooGDB) with online access at www.bamboogdb.org. BambooGDB contains three types of datasets, (a) high-quality genome sequence data, (b) full-length cDNA data, and (c) deep RNA-sequencing data. It provides a productive platform for comparative genomic analysis, protein–protein interaction studies, pathway analysis, and graphical visualization. Further, the database serves as a source of for identifying bamboo microsatellites (simple sequence repeats, SSR), although SSR frequency is lower (Table 1) than that of the rice, sorghum, purple false brome, and *Arabidopsis* (Zhao et al., 2015).

Ma et al. (2018) constructed another online database, BambooNET, available at bioinformatics.cau.edu.cn/bamboo. This database is enriched with datasets for coexpression network analysis, *cis*-elements, functional modules, and gene set enrichment analysis (GSEA) tools using moso bamboo sequences. With the very recent release of four draft genomes of major bamboos (Guo, Ma, et al., 2019) representing three ploidy levels, *Bonia amplexicaulis* (hexaploid, $2n = 72$, paleotropical woody bamboo), *Guadua angustifolia* (tetraploid, $2n = 46$, neotropical woody bamboo), and *Olyra latifolia* and *Raddia guianensis* (diploid, $2n = 22$, herbaceous bamboo) together with that of moso bamboo, the database has been enriched. It was found that woody bamboo had higher number of unique gene families and multigene families than herbaceous bamboos. The diploid bamboo genomes had more single-copy genes, while the polyploid genomes revealed multigene families, with tetraploids having two or more member gene families. Correspondingly, hexaploid bamboos showed higher numbers of multigene families.

3.3 | Multigene families

Multigene families arose during the evolution of moso bamboo, through gene duplication and polyploidization events. These families include cellulose, lignin, and cell wall biosynthesis genes important for active bamboo growth. This has evidently led to the functional diversity of various bamboo species at different levels of growth and metabolism. Among the large multigene families, lignin biosynthesis is the largest pathway genetic system in moso bamboo genome. It has higher number of gene families and coding genes for lignin biosynthesis than do other plant species such as *Amborella trichopoda*, African oil palm, *Arabidopsis*, purple false brome, rice, sorghum, great duckweed, and black cottonwood. A total of 242 genes from 13 gene families are involved in lignin biosynthesis pathways, contributing to functional gene diversity in moso bamboo. Large-scale transcriptome

TABLE 1 The genome size, distribution, frequency, and type of microsatellites in the genomes of six surveyed grass species

Plant species		Identified SSRs			
Common name	Scientific name	Genome size (Mb)	SSR/Mb	Single SSRs (2–6 bp repeat motif), number (%)	Compound SSRs, number (%)
Moso bamboo	<i>Phyllostachys edulis</i>	2,051.7	62.2	106,582 (83.53)	21,011 (16.47)
Maize	<i>Zea mays</i>	2,066.4	52.1	94,683 (87.88)	13,059 (12.12)
Rice	<i>Oryza sativa</i>	374.5	165.5	49,505 (79.88)	12,472 (20.12)
Sorghum	<i>Sorghum bicolor</i>	738.5	91.1	57,016 (84.70)	10,295 (15.30)
Purple false brome	<i>Brachypodium distachyon</i>	271.9	76.5	17,865 (85.93)	2,924 (14.07)
<i>Arabidopsis</i>	<i>Arabidopsis thaliana</i>	119.7	135.5	12,259 (75.59)	3,958 (24.41)

Source: Zhao et al., (2015), <https://doi.org/10.1038/srep08018>

analysis of 26 representative bamboo tissues revealed AS profile of 25,225 splicing genes, including lignin biosynthesis pathway genes from 10 families (Zhao, Gao, et al., 2018).

4 | PROSPECTS FOR GENOMICS-ASSISTED BREEDING

4.1 | Molecular markers

Use of molecular marker systems has led to significant advancements in understanding of evolutionary relations among the bamboo through genetic diversity studies, which was highly constrained earlier with the limited morphological characteristics (Das, Bhattacharya, Singh, Filgueiras, & Pal, 2008). Several marker systems have been employed in deciphering the genetic diversity of bamboos (Yeasmin et al., 2015), which included morphological, biochemical, and molecular markers. Investigating in a community of *Phyllostachys pubescens*, Isagi et al. (2004) suggested that clonal structure of populations has to be the main motive of bamboo diversity studies, as bamboos have evolved with natural proclivity for vegetative propagation. Earlier to this, Chao and Tang (1993) opined to use marker-based genetic analyses to resolve the complexity in bamboo classification and taxonomy. Previous to the use of DNA-based marker systems, there were few studies that used biomarker systems such as secondary metabolites such as flavonoids (Chou & Hwang, 1985; Chou, Sheen, & Hwang, 1984; Li, 1990), volatile compounds (Chen & Lu, 1994), and isozymes (Chou, Yang, & Sheen, 1984; Chu, Chou, Li, Shih, & Woo, 1972; Wang et al., 1980, 1983). Different enzymes investigated were peroxidases (Chou, Sheen, et al., 1984; Li, 1989), esterase (Li, 1989), transaminases (Huang & Murashige, 1983), dehydrogenases (Gielis, Everaert, Goetghebeur, & Deloosse, 1997), and multiple enzyme systems (Huh & Huh, 2002).

The first report of the use of DNA-based markers came from Friar and Kochert (1991), after they analyzed 42 accessions belonging to six genera and about 25 species using restriction fragment length polymorphisms (RFLPs). They reported significant species-specific polymorphism in the nuclear DNA, but relatively little variation in the chloroplast DNA (cpDNA). However, Watanabe, Ito, and Kurita (1994) used cpDNA diversity using 15 restriction enzymes to draw the phylogeny of bamboo and reported two major lineages. Although the studies using organellar genomes are limited, full-length cpDNA information was used to study moso bamboo's relationship with other bamboo species (Ma, Zhang, Zeng, Guo, & Li, 2014; Wysocki, Clark, Attigala, Ruiz-Sanchez, & Duvall, 2015). RFLP markers were used to understand the diversity and evolution within *Phyllostachys* genus and found that species-level delineation is possible using molecular data (Friar & Kochert, 1994). With the

advent of PCR-based markers, Hsiao and Rieseberg (1994) used random amplified polymorphic DNA (RAPD) markers to fingerprint *Yushania* species, while *Phyllostachys* cultivars and species were analyzed for developing an identification system (Ding, 1998; Gielis, 1995; Gielis et al., 1997).

The application of second-generation molecular markers on 176 genotypes of the moso bamboo was reported in 1997 (Table 2), wherein 13 RAPD, three SSRs, and one minisatellite markers were used to conclude that RAPD is the suitable marker to identify clones and to unravel genetic relationship between moso bamboo cultivars (Lai & Hsiao, 1997). Later, Gielis (1998) foresaw the opportunity for resolving several taxonomic problems with the help of molecular data within the *Phyllostachys* genus, particularly using RAPD markers. Nayak, Rout, and Das (2003) utilized RAPD markers to distinguish genera such as *Bambusa*, *Dendrocalamus*, *Dinocloa*, and *Cephalostachyum*. Other studies that applied RAPD markers for bamboo diversity analysis include Ramanayake, Meemaduma, and Weerawardene (2007). From the random amplified products, later, sequence characterized amplified region (SCAR) markers specific to *Bambusa balcooa* were developed for distinguishing species (Das, Bhattacharya, & Pal, 2005). Ruan et al. (2008) studied the genetic relationships within moso bamboos from 17 provinces of China using AFLP and ISSR markers but reported low polymorphism at the species level. Among the second-generation marker systems, amplified fragment length polymorphism (AFLP) has been widely used in phylogenetic analysis in bamboos in earlier days (Ghosh, Devi, Mandi, & Talukdar, 2011; Loh, Kiew, Set, Gan, & Gan, 2000; Waikhom, Ghosh, Talukdar, & Mandi, 2012), because of the nonavailability of sufficient number of SSR markers. Suyama, Obayashi, and Hayashi (2000) used AFLP for identifying the clonal diversity of dwarf bamboo, *Sasa senanensis*, from an admixed clonal garden and identified 22 constituent clones in the population. AFLP diversity was found highly discriminatory than internal transcribed spacer (ITS) region of nuclear ribosomal DNA (nrDNA), between *Phyllostachys* and its allied genus for phylogenetic reconstruction at taxonomic level (Hodkinson, Renvoize, Chonghaile, Stapleton, & Chase, 2000). Similarly, in Columbia, AFLP marker system was employed to divulge the genetic relations between accessions and biotypes of *Guadua angustifolia*, American woody bamboo (Marulanda, Márquez, & Londoño, 2002). AFLP fingerprints were also used for understanding the genetic diversity in river cane (*Arundinaria gigantea*) and its relation to sexual reproduction (Katherine, Joseph, Max, Terryol, & Robert, 2009).

Other marker systems that were used in diversity studies of bamboo include intersimple sequence repeat (ISSR) markers (Lin et al., 2010; Mukherjee et al., 2010; Nilkanta, Amom, Tikendra, Rahaman, & Nongdam, 2017; Tian, Yang, Wong, Liu, & Ruan, 2012; Yang, An, Gu, & Tian, 2012). Lin, Ruan, Lou, Guo, and Fang (2009) found that combined

TABLE 2 The details of genetic diversity studies and outputs of moso bamboo genotypes using various molecular markers

Marker type	Number of markers and phenotypes used and major findings of studies	References
RAPD, microsatellite, and minisatellite	Nine clones were identified from 176 Taiwan-based clones. Genetic variation was limited among nine clones. Nantou region of Taiwan might have been the first area of successful cultivation in Taiwan	Lai and Hsiao (1997)
AFLP	Studies of the flowering traits of moso bamboo clones in a plant population where each gene has its individual flowering time	Isagi et al. (2004)
RAPD	The genetic relationship in 18 moso bamboo populations from the mainland of China	Zhang, Ma, and Ding (2007)
AFLP and ISSR	Evaluated phylogenetic variations of moso bamboo from 17 Chinese provenances. Both markers showed significant correlation of genetic relationship of moso bamboo	Ruan et al. (2008)
SSR and EST-SSR	Studies of the transferability of 98 SSR of rice and 20 EST-SSR of sugarcane for genetic diversity studies of moso bamboo. Both rice and sugarcane have high genomic synteny with moso bamboo	Sharma et al. (2008)
AFLP and ISSR	Studies of the genetic similarity of genetic distances among ten cultivars of moso bamboo where cultivars were clearly divided into three groups. AFLP and ISSR markers had a significant correlation	Lin et al. (2009)
EST-SSR	Development of 38,000 EST-SSR markers by full-length cDNAs sequencing of moso bamboo and by using genomic resource database of moso bamboo	Peng et al. (2010)
SSR	The development of SSR markers, detection of polymorphisms, and transferability to six <i>Phyllostachys</i> species	Tang et al. (2010)
SSR and EST-SSR	The rapid development of SSR and EST-SSR markers and detection of polymorphisms	Zhang, Guan, Yang, Yu, and Luo (2011)
SSR	The development of 20 SSR markers and detection of polymorphisms in 71 moso bamboo samples	Jiang et al. (2013)
cpDNA	Full-length cpDNA was isolated, and the deep-level genetic relationship with other bamboo species was studied	Ma et al. (2014)
SSR	Development of SSR markers for the taxonomy of <i>Phyllostachys</i> species. A total of 23 markers were validated in 78 accessions of <i>Phyllostachys</i> species	Zhao et al. (2015)
SSR	The genetic diversity and patterns of clone distribution of 246 samples from 28 wild populations of moso bamboo in China and Japan. Simple genetic structure and low genetic diversity were observed	Isagi et al. (2016)
SSR	The genetic relationship of 803 genotypes of moso bamboo from the main growing regions of moso bamboo in China. AMOVA showed that within the populations, the genetic diversity was higher than among the populations	Jiang et al. (2017)
LTR retroelements	Evolutionary analysis of LTR and phylogenetic analysis in moso bamboo	Zhou, Hu, and Zhu (2017)
SNP	Analysis of genetic variation among moso bamboos through genome resequencing. Total of 4,700,803 Uni-SNPs was identified, and these SNPs were linked with many biological pathways	Zhou, Wu, et al. (2018)
IRAP	The development of IRAP markers for bamboo and analyzed the evolutionary patterns of 58 <i>Phyllostachys</i> species (Asian bamboo) within and among populations using the developed markers	Li et al. (2019)

Note: RAPD, randomly amplified polymorphic DNA; AFLP, amplified fragment length polymorphism; ISSR, intersimple sequence repeat; SSR, simple sequence repeat; EST-SSR, expressed sequence tag SSR; cDNA, complementary DNA; cpDNA, chloroplast DNA; AMOVA, analysis of molecular variance; LTR retroelements, long terminal repeat retroelements; Uni-SNPs, unique single nucleotide polymorphisms; Uni-Indels, unique InDels; IRAP, inter-retrotransposon amplified polymorphism.

use of 16 ISSR and AFLP markers in ten moso bamboo cultivars revealed higher polymorphism than using single marker system. The markers clearly clustered ten cultivars into 3 groups, highlighting the genetic resemblance between cultivars in each group. Afterward, combined use of marker

systems has been used in several studies such as RAPD-AFLP (Nag et al., 2013), RAPD-ISSR (Desai et al., 2015), RAPD-RFLP (Konzen, Perón, Ito, Brondani, & Tsai, 2017), RAPD with morphological traits (Shalini, Meena, Tarafdar, & Thakur, 2013), and morphological traits with

sequence-related amplified polymorphism (SRAP) markers (Zhu, Liu, Tang, Fu, & Tang, 2014). Genetic diversity between cultivars of *Phyllostachys violascens* was reported using combinations of ISSR, AFLP, and SRAP markers (Lin et al., 2011). While reviewing the genetic fidelity of the bamboo species resolvable by the molecular markers, Singh et al. (2013) suggested that such markers could be put into use for characterizing somaclonal variants of moso bamboo.

Unlike in other cereal crops, the initial phase of marker-based studies on genetic diversity did not find a place for the use of SSR markers in bamboos, primarily due to the absence of genomic information. However, using the advantage of cross-genome portability especially within the grass family Poaceae, the first kind of SSRs employed for molecular systematic studies in bamboo was derived from rice (Li, Yin, Zou, Ding, & Huang, 2002). Following this, Chen et al. (2010) could demonstrate 68% cross-transferability of rice SSRs was among bamboo accessions. Among the various markers used in investigating moso bamboo, several ESTs and SSR markers derived from grass genomes have been used (Jiang, Zhang, & Ding, 2013; Lin et al., 2006, 2014; Peng et al., 2010; Tang, Lu, Fang, Zhang, & Zhou, 2010; Zhao et al., 2015). Cross-genome derived expressed sequence tag (EST)-SSRs were experimented by Barkley, Newman, Wang, Hotchkiss, and Pederson (2005) who used twenty-five markers from maize, sorghum, wheat, and rice to study the genetic diversity among 92 bamboo accessions. They found that these markers could resolve the panel into two clusters, corresponding prominently to their morphological pattern. Later, Sharma et al. (2008) ventured to use cross-genome-compatible SSRs derived from rice and sugarcane and found that at least 42% of SSRs from rice and 75% of EST-based SSRs from sugarcane could amplify among the 23 bamboo species studied. Further, they reported that 70% of the polymorphic markers were suitable for species characterization. Gui et al. (2010) reported high genomic synteny of rice and sorghum with moso bamboo opening up the possibility of using this information as a model for genome decoding. Cross-species-derived EST-SSRs obtained from *Bambusa oldhamii* showed transferability of 30%–100% among different bamboo species, ascertaining their usability in diversity studies (Sharma et al., 2009). Following the reports of full-length cDNA and ESTs from moso bamboo (Peng et al., 2010) and full chloroplast genomes of six bamboo species (Zhang, Ma, et al., 2011), ubiquitous presence of SSR markers across bamboo genome was reported (Zhou, Liu, & Tang, 2011). Fifteen EST-SSRs from *Bambusa edulis* and *B. oldhamii* were shown to be ~60% transferable to moso bamboo (Dong, Wu, Lin, Zhou, & Tang, 2011). Subsequently, more bamboo-based EST-SSRs were also reported by Ramalakshmi and Piramanayagam (2010) and Cai et al. (2019). Dong, Zhang, and Yang (2012) used sixteen bamboo-specific SSRs for assessing the genetic structure of *D. sinicus*.

Genome-wide SSR markers were identified only following the release of the moso bamboo draft genome of by Peng, Lu, et al. (2013). Prior to this, only a few bamboo-derived SSRs were available for diversity studies (Kaneko, Franklin, Yamasaki, & Isagi, 2008; Kitamura, Saitoh, Matsuo, & Suyama, 2009; Nayak & Rout, 2005). Zhao et al. (2015), for the first time, developed genome-wide SSR markers using 127,593 SSR motifs identified across the moso bamboo genome. They have designed 1,451 primers of which 1,098 markers were physically mapped, and among which 917 markers could be validated in 9 accessions with 39.8% transferability. Afterward, a subset of 24 SSRs from the valid set could differentiate an assembly of 78 accessions to their taxonomic configuration. Recently, Jiang et al. (2017) studied the genetic relationship of 803 moso bamboo genotypes from 34 populations from China using 20 fluorescently labeled SSR markers. Population structure analysis showed that the 803 genotypes clustered into two subpopulations, with a within-population genetic diversity of 84.6%. Both model-based and graphical diversity analyses led to similar results of this population, implying rapid spread of bamboo throughout mainland China, predominantly through clonal propagation with limited cycles of sexual reproduction. The study also suggested the prospective use of germplasm collection in moso bamboo development, and of the possibility of uncovering greater genetic diversity by using dense markers with genome-wide coverage.

Double-digest restriction site-associated DNA (ddRAD) markers have genome-wide coverage due to sampling of the whole genome for restriction sites of a frequent-cutter endonuclease. This technique is a reduced dimension sequencing approach and is widely used for SNP identification and genotyping (Baird et al., 2008; Davey et al., 2011). Yang et al. (2016) advocated the usefulness of ddRAD markers for plant phylogenetic analysis by developing a universal and simplified ddRAD library and demonstrated that these markers could delineate the phylogenetic relationship between two woody bamboos, *Dendrocalamus* and *Phyllostachys*. Further, ddRAD markers were used for phylogenomic analysis of *Shibataea* genus bamboos to reveal intraspecific gene flow during sympatric speciation (Guo, Guo, & Li, 2019). Similar evolutionary studies were followed using ddRAD markers in other bamboo genera, such as temperate bamboos (Wang, Zhao, Eaton, Li, & Guo, 2013), alpine bamboos (Ye, Ma, et al., 2019), *Bambusa–Dendrocalamus–Gigantochloa* complex (Liu, Zhou, et al., 2020), and woody bamboos (Guo, Ma, et al., 2019).

In recent years, whole-genome sequencing and cpDNA have been used for genetic diversity assessment in moso bamboo. The genome resequencing revealed a total of 4,700,803 unique single nucleotide polymorphisms (Uni-SNPs) and 268,150 unique InDels (Uni-Indels) in moso bamboo. These

Uni-SNPs and Uni-Indels were linked with pathways such as caffeine metabolism, ribosome biogenesis, and anion binding (Zhou, Wu, et al., 2018). Very recently, we have developed 16 inter-retrotransposon amplified polymorphism (IRAP) markers for the first time in bamboo (Li et al., 2019). Using these markers on genetic diversity and population structure divided the 58 Asian bamboo accessions (*Phyllostachys*) into four subpopulations, PhSP1, PhSP2, PhSP3, and PhSP4. These markers highlight the usability of a retrotransposon-based marker systems in determining the interspecific variability of bamboos.

4.2 | Map of bamboo genome

Apart from the paucity of genome-wide molecular markers, attempts to map bamboo genomes confronted another big challenge, the absence of mapping populations. Most of the bamboos being monocarpic and considering the long life cycle that extends up to 100 years, the prospect of developing conventional mapping populations as done in annual cereals is improbable. The only option is to look for inbred population developed from a flowering clone that may segregate for some of the loci, the extend of which depends on the heterozygosity in the mother clone. Therefore, earlier attempt to map the bamboo genome remains obscure, until the development of genome-wide markers. The first study of a high-density genetic map of bamboo came recently (Guo, Ma, et al., 2019) reported from an inbred population of 190 progenies of ma bamboo (*Dendrocalamus latiflorus* Munro) using 3,627 ddRAD markers. The genetic map showed 36 linkage groups corresponding to the 36 chromosome pairs covering 93.3% of the genome. The total map length was 3,113 centimorgans (cM), with an average marker distance of 0.93 cM per marker. The length of the linkage groups ranged between 4.91 and 131.69 cM. A total of 720 (19.9%) markers showed high synteny between ma bamboo and the rice genome. The comparative analysis supported a hexaploid origin of ma bamboo. In addition, the scaffolds of assembled sequences of the *B. amplexicaulis* were aligned with the genetic map of ma bamboo, showing that 244 scaffolds covering 481.40 Mb matched with 72.0% consanguinity, confirming high level of congruence between the ddRAD data and the assembled sequences. Besides, Guo, Ma, et al. (2019) reported noncoding RNAs such as microRNA (miRNA), ribosomal RNA (rRNA), transfer RNA (tRNA), small nuclear RNA (snRNA), and small nucleolar RNA (snoRNA) genes across bamboo genomes. These genetic resources will be useful for in-depth studies and analyses of the transcriptome, DNA methylation, and histone modification of the bamboo genomes.

4.3 | Transposable elements

Transposable elements (TEs, jumping genes, or transposons) are innate genetic elements that move around the genomes of higher plants (McClintock, 1984) and often considered as evolutionary signatures (Feschotte & Wessler, 2002; Jurka, Kapitonov, Kohany, & Jurka, 2007). Although their specific functions within the genome remain enigmatic, TEs are known to create spontaneous genomic variations by their transposition behavior (Bourque et al., 2018). Recent advancements in molecular diagnostics recruit TEs as tools for studying genome-level variation, evolution, gene tagging, and targeted gene silencing, which overall can facilitate crop improvement (Cho, 2018; Joly-Lopez et al., 2017; Makarevitch et al., 2015). TEs are predominantly divided into two classes, class I elements or retrotransposons and class II elements or DNA transposons (Bourque et al., 2018). Genome of higher plants usually possess large proportion of TEs, particularly of retrotransposon families. In the moso bamboo genome, TEs account for 63.3% (Zhao, Gao, et al., 2018), which is relatively lower than that in the maize genome (85%) (Schnable et al., 2009) and similar to that in the sorghum genome (62%) (Paterson et al., 2009). However, the moso bamboo genome possesses higher proportion of TEs than rice (40%) (Goff et al., 2002) and *Brachypodium* (28%) genomes (Initiative, 2010). In bamboo species, the TE contents correlate with the genome sizes (Guo, Ma, et al., 2019; Li, Shi, et al., 2020) of six bamboos, *B. amplexicaulis*, *G. angustifolia*, *O. latifolia*, *R. guianensis*, *R. distichophylla*, and moso bamboo, indicating that the TE proliferation might have been the major driver of bamboo species evolution (Wicker et al., 2007). Among these, *G. angustifolia* and moso bamboo contain more TEs (Guo, Ma, et al., 2019). In the study of Zhao, Gao, et al. (2018) that thoroughly interrogated TEs in the moso bamboo genome, TE insertions were frequently found around the flanking regions of 26,366 genes, which is 51.6% of the entire genes annotated in the moso bamboo genome. The total length of the inserted TEs around bamboo genes is ~46 Mb, and the highly conserved genes are associated with more TEs. Interestingly, the genome-wide analysis showed that LTR retroelements locate distantly from genes and exhibited substantially strong transcriptional activity. The divergence rate of TEs was estimated as 30%, suggesting ancestral origin of TE insertions. Among the different classes of TEs in the moso bamboo genome, retrotransposons accounted for 45.7% of the entire genome, followed by DNA transposons (10.4%), and the remaining 7.2% was unclassified. Among the retroelements, 43.9% was long terminal repeat (LTR) elements, 1.7% was long interspersed nuclear elements (LINEs), and 0.03% are short interspersed nuclear elements (SINEs).

The LTR families are the most dominant species among the retrotransposons representing over 50% of all TEs. Particularly, *Ty3-gypsy* and *Ty1-copia* are found to have the highest copy numbers (Peng, Lu, et al., 2013; Zhao, Gao, et al., 2018). Given that LTR retrotransposons play significant roles in bamboo genome evolution (Li, Ramakrishnan, et al., 2020), *Ty3-gypsy* and *Ty1-copia* elements are thought to be responsible for enlarging the genome size of moso bamboo (Zhou, Hu, & Zhu, 2017; Zhou, Zhong, Zhang, Tang, & Tang, 2010). Moreover, the LTRs produce more than 30% of small interfering RNAs (siRNA) in the moso bamboo (Zhou, Zhu, Bai, Hänninen, & Meng, 2017) that might contribute to diversification of gene regulatory network. Intriguingly, an active LTR retroelement, *Phyllostachys heterocycla* retrotransposon 2 (*PHRE2*), increased its copy number when transgenic *Arabidopsis* plants carrying *PHRE2* were challenged with environmental stresses, gamma ray irradiation, and plant hormones (Zhou, Liang, & Hänninen, 2018). Such transposition behavior upon specific external stimulation potentiates the usage of a particular family of retrotransposon as breeding resource that creates novel agronomic alleles and rewire gene regulatory network. In moso bamboo, 4.7% of the genome is accounted by nonautonomous transposon-like *miniature* inverted-repeat transposable elements (*MITEs*) from which massive small RNAs are originated (Zhou, Tao, et al., 2016). Among the TEs found around the promoter regions, approximately 85.7% were from three families (Zhou, Zhou, & Hänninen, 2018), *hAT*-like transposons, *MITEs*, and *SINEs*. The presence of *MITEs* in the promoter regions is associated with gene repression (Zhou, Chen, Chen, Zhou, Tang, & Hänninen, 2017), presumably through the establishment of the epigenetic silencing mediated by siRNAs targeting TEs.

DNA transposons of moso bamboo are the most widely studied among the bamboo TEs (Zhong, Zhou, Xu, & Tang, 2010; Zhou, Liu, & Tang, 2012; Zhou, Lu, Zhong, Liu, & Tang, 2010; Zhou, Lu, Zhong, Tang, & Tang, 2010; Zhou, Zhong, & Tang, 2011). They are classified to three superfamilies: *mariner*-like elements (*MLE*), *P* instability factor (*PIF*)-like elements, and *Pong*-like elements. Extensive phylogenetic studies carried out in 38 genera of the Bambusoideae subfamily revealed that DNA transposons are rather widespread, abundant, and diverse among the bamboos. Among the TEs in the bamboo genome, *MLEs* are thought to be most active in transposition, presumably because they contain the intact DNA-binding motifs, DD39D catalytic domains, and only a few notable frameshifts (Zhou, Zhong, et al., 2011). Indeed, two distinct full-length *MLEs* from moso bamboo, *Ppmar1* and *Ppmar2* (Zhou, Zhong, Hu, & Tang, 2015), exhibited active transposition in yeast and *Arabidopsis* plants (Zhou, Hu, Liu, & Tang, 2016; Zhou, Hu, Miskey, et al., 2017). Both *Ppmar1* and *Ppmar2* preferably inserted into TA-rich regions, into or near genes, implicating their relevance to

gene regulation. Previous studies attempted to understand the transposition control of *MLEs*. Ramakrishnan, Zhou, Pan, Hänninen, Yrjälä, et al. (2019) were able to alter the transposition frequency of *Ppmar2* by 1.5–2.0 times more than that of the wild-type yeast by increasing the affinities of terminal inverted repeats (TIRs) toward the DNA-binding domain of TPase. Further, the nuclear export signal (NES) domains of both *Ppmar1* and *Ppmar2* elements regulate the nuclear export of TPases that ultimately influences the transposition activity of *MLEs* (Ramakrishnan, Zhou, Pan, Hänninen, Tang, et al., 2019). Altogether, TEs are potent gene regulators in the moso bamboo genome that vastly alter genetic and epigenetic architecture. Given that most TEs are controllable by certain environmental stimuli, TEs are obviously attractive breeding agents that will allow us to manipulate the bamboo genome and extend the pool of genetic variations. Advances of our understanding of TEs will greatly enhance the genetic improvement of bamboo.

5 | DEVELOPMENT OF GENOMIC RESOURCES FOR IDENTIFYING GENES UNDERLYING KEY TRAITS

5.1 | Transcription factors

Transcription factors (TFs) are DNA-binding proteins that control gene transcription in order to regulate gene expression. There are several of them in the genomes of higher organisms that work in a coordinated fashion. In moso bamboo genome, a total of 1,771 TFs were reported using transcriptome sequencing (Zhao, Dong, et al., 2016), which showed various expression patterns in different tissues collected from leaf, rhizome, root, shoot, and panicle (Table 3). Classified into 54 families, several of the TFs belonged to large gene families such as MYB (myeloblastosis), NAC (no apical meristem, NAM-*Arabidopsis* transcription activation factor, ATAF-cup shaped cotyledon, CUC), WRKY (tryptophan-arginine-lysine-tyrosine), AP2/ERF, ARF (auxin response factor), bZIP (basic leucine zipper), G2 (golden2)-like, bHLH (basic helix-loop-helix), and HD-ZIP (homeodomain-leucine zipper). Later, using the iTAK database (<http://bioinfo.bti.cornell.edu/cgi-bin/itak/index.cgi>), Zhao, Gao, et al. (2018) identified 3,497 TFs belonging to 69 families from the chromosome-level reference genome of moso bamboo. Among these, four TF families, bHLH, MYB, AP2/ERF, and NAC, had more than 240 TFs, and six families, C3H (Cys3His zinc finger domain containing protein), MYB-related, GRAS (gibberellic acid insensitive, GAI-resistance gene analogue, RGA-SCARECROW, SCR), bZIP, C2H2 (Cys2His2-like fold group zinc finger protein), and WRKY, had between 100 and 200 TFs. The remaining families had less than 100 TFs. Comparatively, moso bamboo

TABLE 3 Details of transcription factors (TFs) identified in moso bamboo under different experimental conditions, and their functions identified using model organisms

Name of TFs	Gene functions	Overexpression study in model organisms	Major findings	References
DREB	Regulates stress-related genes and improves plant resistance to abiotic stress	NA	Two <i>PeDREB2A</i> and <i>PeDREB1A</i> genes were isolated, and their proteins have typical AP2/ERF domains. The qRT-PCR analysis revealed that these genes have different expression profiles in different tissues under cold, drought, and salt stresses, respectively	Wu, Li, et al., 2015
AP2/ERF	Regulation of growth and development, and response to biotic and abiotic stresses	NA	The phylogeny analyses classified 116 AP2/ERF genes into three subfamilies (AP2, RAV, and ERF). The evolutionary analysis showed that the division time of <i>PeAP2/ERF</i> genes of rice from moso bamboo was 15–23 Mya	Wu, Lv, et al., 2015
GRAS	Plant growth and development, disease resistance, response to abiotic stress	NA	The expression profiles of <i>PeGRASs</i> in response to high light treatment. Expression pattern of <i>PeGRASs</i> classified/categorized profiles into 6 groups forming a coexpression network	Zhao, Dong, et al., 2016
TIFY	Response to dehydration and cold stress		More than 50% of <i>PeTIFY</i> genes were up-regulated during dehydration and cold stress	Huang, Jin, et al., 2016
SBP-like	Plant growth, flower development, and signal transduction	NA	The phylogeny analysis showed that SBP-like and SBP proteins clustered similar to those in rice and maize. SPL genes were highly expressed in flowers and leaves	Pan et al., 2017
WRKY	Multiple biological processes	<i>Arabidopsis</i>	The qRT-PCR expression pattern showed different expression under abiotic stress. <i>PhWRKY72-2</i> reduced seedling of transgenic drought stress response	Li et al., 2017
MADS-box genes	Flower development and regulation of floral organ identity	<i>Arabidopsis</i>	Earlier flowering and the development of an aberrant flower phenotype	Cheng et al., 2017; Zhang, Tang, et al., 2018
WRKY	Plant development and response to biotic and abiotic stress	<i>Arabidopsis</i>	<i>PeWRKY83</i> in <i>Arabidopsis</i> produced better physiological properties than wild type under salt stress, and transgenic plant produced more endogenous ABA by regulating ABA synthesis	Wu et al., 2017
bHLH	Plant growth and biotic/abiotic stress		Differentially regulated in tissues after abscisic acid, drought, and methyl treatment	Cheng, Xiong, et al., 2018
Dof	Plant growth, development, and response to abiotic stress	NA	Showed different expression patterns under cold, salt, and drought stresses. The coexpression network showed <i>PhDof12</i> , <i>PhDof14</i> , and <i>PhDof16</i> play a significant role in flower development	Cheng, Hou, et al., 2018
PHD-finger	Organ formation and response to various environmental stress	NA	The <i>PePHD</i> genes were differentially regulated in leaves under drought, abscisic acid, NaCl, and cold treatments	Gao, Liu, Wang, Li, & Xiang, 2018

(Continues)

TABLE 3 (Continued)

Name of TFs	Gene functions	Overexpression study in model organisms	Major findings	References
TCP	Plant and growth development, and response to environmental stress	NA	The <i>PeTCP</i> members were highly expressed in response to abscisic acid, methyl jasmonate, and salicylic acid treatments. The <i>PeTCP</i> played a significant role in plant hormone transduction for growth and development and in response to abiotic stress	Liu, Wu, et al., 2018
Zinc finger	Drought and salt tolerance	<i>Arabidopsis</i> and rice	<i>PeDil9-4</i> enhanced drought and salt tolerance via the ABA-dependent signaling pathway and higher ABA accumulation in transgenic plants	Wu et al., 2018
TTF	Different developmental stages	NA	<i>TTF</i> , involved in response to stress conditions, had higher expression in leaves and panicles. <i>PeTTF29</i> has transcriptional activity	Cheng, Xiong, et al., 2019
MYB	Cell formation, morphogenesis, and signal transduction	NA	<i>PeMYBs</i> are different in exon numbers and were shown to have differential expressions in leaves, panicles, shoots, and rhizomes. <i>PeMYBs</i> play a fundamental role in secondary cell wall formation and shoot lignification	Yang, Li, et al., 2019
MYB	Abiotic stress resistance and development	<i>Arabidopsis</i>	Moso bamboo has <i>R2R3MYB</i> genes of ancient origin. These genes were involved in response to both various abiotic stress, flower development, protein interaction network. <i>PhMYB4-1</i> gene showed resistance to cold stress in <i>Arabidopsis</i> seedlings	Hou et al., 2018
GATA	Rhizome development and shoot growth	<i>Arabidopsis</i>	The promoter region of the <i>PeGATA</i> genes has a light, hormone, and stress-related cis-elements. The <i>PeGATA</i> genes showed different expression pattern during the rapid growth of shoots. <i>PeGATA</i> reduced the <i>Arabidopsis</i> ' root growth and shoot growth	Wang, Yang et al., 2019
BZR1	Rapid growth of shoot	<i>Arabidopsis</i>	<i>PeGSK1</i> negatively regulated BZR1-dependent growth-promoting genes in <i>Arabidopsis</i>	Wang, Li et al., 2019
GRF	Hormone regulation during plant development	<i>Nicotiana benthamiana</i> and yeast	<i>PeGRF11</i> was localized in the nucleus of tobacco leaves and interacted with <i>PeGIF3</i> in yeast nucleus	Shi et al., 2019
TCP	Drought tolerance and ABA sensitivity	<i>Arabidopsis</i> , rice, and yeast	<i>PeTCP10</i> conferred drought tolerance of transgenic. Yeast one-hybrid and EMSA assays showed that the direct target of <i>PeTCP10</i> is stress-/ABA-responsive gene BT2	Liu, Gao, et al., 2020

Note: DREB, dehydration-responsive element binding; MADS, minichromosome maintenance 1, agamous, deficient, and serum response factor; bHLH, basic helix-loop-helix; Dof, DNA binding with one finger; AP2/ERF, APETALA2/ethylene response factor; PHD, plant homeodomain; BZR1, brassinazole-resistant-1; *PeGSK1*, GSK3/shaggy-like kinase 1.

genome possesses more TFs than that of *Arabidopsis*, purple false brome, rice, sorghum, foxtail millet, and maize (Zhao, Gao, et al., 2018).

TFs regulate several ontogenetic behaviors in bamboo, especially those are environmentally triggered. Conditional and tissue-specific gene expression requires strong regulatory network of genes (Liu, Gao, et al., 2020). One such trait is flowering behavior, wherein at least 1,768 TFs belonging to 54 families have been identified in moso bamboo (Peng, Lu, et al., 2013). They found that 30% of flowering-related genes were heat-shock protein genes, TFs, and stress-related genes underscoring the environmental regulation of flowering behavior. Among the TFs, MADS (minichromosome maintenance 1, *MCM1*–*agamous*–*deficiens*–*serum response factor*) box genes showed expression patterns were similar to those in *Arabidopsis* and rice. Overexpression of moso bamboo MADS box genes, *PheMADS15* and *PeMADS5* in *Arabidopsis*, showed to induce an early flowering phenotype (Cheng et al., 2017; Zhang, Tang, Lin, Ding, & Tong, 2018). In a recent study on the rapid growth of bamboo, Wang, Li et al. (2019) suggested that the brassinazole-resistant (BZR) TF, *PeBZR1*, is one of the key regulators during the rapid growth. Furthermore, the overexpression of GSK3/shaggy-like kinase 1 (*PeGSK1*) in *Arabidopsis* negatively regulated BZR1 TF-dependent cell growth genes. Similarly, the TF, growth-regulating factor (GRF), is essentially required during bamboo's developmental stages, such as during leaf and early panicle development, wherein *PeGRF* genes were found highly expressed in moso bamboo. By overexpressing *PeGRF11* gene in *Nicotiana benthamiana*, Shi et al. (2019) found that it played a prominent role in hormone regulation. Thirty-one GATA-binding TFs were reported to regulate bamboo shoot and rhizome growth, as observed from the repression of primary root length and plant height in *Arabidopsis*, when one of the genes *PeGATA26* was overexpressed (Wang, Yang et al., 2019).

The TFs also play a significant role in stress response in bamboos. A total of 448 *bHLH* genes falling under 21 sub-families have been identified in moso bamboo, which were shown to be differentially expressed following drought and abscisic acid and methyl jasmonate treatments by qRT-PCR analysis (Cheng, Xiong, et al., 2018). Likewise, 121 genes belonging to WRKY family have been identified in moso bamboo, and through qRT-PCR, the expression pattern of some these genes was shown to vary under abiotic stress. WRKY genes, one of the largest families in higher plants, are implicated in numerous biological processes. In *Arabidopsis*, the overexpression of *PheWRKY72-2* was found to decrease the early growth stage drought stress response in seedlings (Li et al., 2017). Furthermore, 35 members of trihelix transcription factors (TTFs) were observed to show higher expression in bamboo leaves and panicles in response to drought and salt stress treatments (Cheng, Xiong, et al., 2019). Liu, Wu, et al.

(2020) recently identified that TF responses to cold stress are specific to moso bamboo. Since the TFs act as regulatory switches for gene expression, both temporal and spatial, they are critical in understanding the fast growth, flowering behavior, and stress response in bamboos. Recently, studies oriented toward understanding the molecular physiology of woody bamboos have gained pace to boost the industrial use of such bamboo species.

5.2 | MicroRNAs and circular RNAs

Another critical regulatory element in higher plant genomes is noncoding RNAs. They are small but powerful in regulating plant growth and development. The first successful report on noncoding RNAs, particularly miRNAs, of bamboo (ma bamboo) was reported by Zhao, Chen, Peng, Wang, and Gao (2013). In this study, 81 novel miRNAs (76 mature miRNAs and five star miRNAs) and 84 conserved miRNAs (54 mature miRNAs and 30 star miRNAs) belonging to 17 families were identified in leaf tissues by deep sequencing. miRNAs are endogenous, 21 nucleotide-long genetic elements, which act as a negative regulator of their target genes and are involved in a series of developmental processes. Following the success of Zhao, Chen, et al. (2013) report, in moso bamboo, He, Cui, Zhang, Duan, and Zeng (2013) first identified 732 miRNAs and 453 novel miRNAs and studied their expression profiles during culm development. Similarly, a total of 75 miRNAs and 24 miRNA variants of 22 families have been identified in moso bamboo roots and seedlings using NGS, and their mRNA targets were predicted (Xu et al., 2014). For instance, the target of *PedmiR164b* was identified as *PeSNAC1* gene that play an important role in plant development, drought, and salinity tolerance (Wang et al., 2016).

In the moso bamboo genome at chromosome-level assemblies, Zhao, Gao, et al. (2018) recently identified various types of noncoding RNAs, and among them, snRNA had the highest copy numbers (910), followed by tRNA (881), rRNA (408), and miRNA (349). The miRNA expression also alters the morphological and physiological characters of plants (Liu, Yu, Tang, & Huang, 2018). Cheng, Hou, et al. (2019) identified 152 novel miRNAs from 26 miRNA families and demonstrated that miRNA159 played an essential role in stamen development through in situ hybridization. The overexpression of *PhemiR159* reduced anther development and fertility in *Arabidopsis* by regulating the expression of *AtMYB33* TF. Flowering is an important feature where differential expression of miRNAs is observed in moso bamboo. Studies on tissues collected during nonflowering and flowering phases revealed a total of 492 differentially expressed novel miRNAs and 409 known miRNAs, which could be further validated using qRT-PCR assays (Gao et al., 2015). During floral initiation, miRNAs such as *miR159a.1*,

miR160a, *miR168-3p*, *miR390a*, *miR393*, and *miR5139* were found to play key roles through regulatory pathways in moso bamboo. Among these, *miR390a* and *miR5139* were involved in plant–pathogen interactions, *miR160a* and *miR393* were involved in hormone signal transduction, and *miR159a.1* and *miR168-3p* were found to have a regulatory role in the endoplasmic reticulum during protein processing (Ge et al., 2017).

Not known until recently, circular RNAs (circRNAs) are a class of noncoding RNAs that are believed to have regulatory functions. Although their exact functions are still under debate, circRNAs are known to as a “sponge” for miRNAs (Dori & Biciato, 2019; Hansen et al., 2013). This sponging function is due to the presence of several miRNA response elements (MREs) that bind with a particular type of miRNA. Very recently, using NGS technology, Wang, Gao, et al. (2019) identified 895 circRNAs in moso bamboo, generated from 759 coding genes involved in the lignin, cellulose, and hemicellulose biosynthetic process. These circRNAs interact with miRNAs to regulate their associated linear mRNAs. In-depth studies on miRNAs and circRNAs in bamboos could throw light on complex regulatory patterns for the developmental mechanisms and also for the expression of traits of industrial relevance.

5.3 | Genome-wide global and conditional coexpression networks

To unfurl the complexity in gene expression, an analysis of their coexpression network is a promising route (Zinkgraf, Gerttula, Zhao, Filkov, & Groover, 2018). To achieve this, a complementary approach has successfully been used: the cross-species gene network inference. This could not only can aid to resolve networks at a finer level but also can help in identifying genes that are hitherto not mapped. In this approach, transcriptome assemblies of two or more species are considered together to chart the expression sequences common to all species and responses that are species-specific. Zinkgraf, Groover, and Filkov (2018) proposed a tool, fastOC, for the gene coexpression network analyses across multiple species. Initial evidence shows that the tool works effectively in calculating coexpression modules with minimal computing requirements, thus making cross-species gene network comparison practical.

A large amount of moso bamboo transcriptome datasets are currently available from different developmental stages and under different stress conditions. From the potential benefits of the coexpression network analysis, it is possible to utilize these data to construct coexpression networks for a better understanding of the molecular mechanisms of moso bamboo ontogeny and development at different growth stages (Figure 2). Following these lines, Ma et al. (2018) constructed the coexpression network of moso bamboo

using genome sequences and 78 transcriptomes. They built genome-wide global and conditional coexpression networks and identified 1,896 functional modules associated with bamboo growth and development. This has led to the building of BambooNET, an online database for moso bamboo coexpression network available at <http://bioinformatics.cau.edu.cn/bamboo>. The site also offers free module enrichment analysis, cis-element analysis, gene sets analyses, and other functional tools. New opportunities have emerged after the availability of the moso bamboo's reference genome, together with the draft genomes of four major bamboos, including *B. amplexicaulis*, *G. angustifolia*, *O. latifolia*, and *R. guianensis*, as well as the moso bamboo's transcriptome database and BambooNET (Figure 3).

5.4 | Transcriptomes and proteomes

Gene expression products are important indicators of genetic functions in an organism, growth, development, sustenance, stress alleviation, and reproduction. Genome-wide expression products can be compartmentalized with respect to three levels of their development, such as transcriptomes, proteomes, and metabolomes. Transcriptomes are the array of transcription products, processed mRNAs that are produced at different levels of organization, either constitutive (global) or tissue/stage/environment-specific (conditional). Transcriptomes are indicators of the immediate genome response and therefore can significantly lead to genes responsible for organism's behavior (Gao, Zhao, & Tang, 2018). In moso bamboo, paired-end RNA-seq libraries were prepared by sequencing transcriptomes from young leaves, rhizomes, roots, internodes, shoots, flower panicles, flowers, sheaths, buds, etc. The transcriptome assembly was then compared with whole-genome sequences for identification. The whole analysis required next-generation platforms such as Illumina HiSeq™ 2000, or 2,500, or 4,000 (Illumina, San Diego, CA, USA) and Roche 454 GS FLX, for sequencing, alignment, and gene ontology studies using the Kyoto Encyclopedia of Genes and Genomes (KEGG) pathway, etc., The moso bamboo draft genome was mostly used as a reference genome for assembling the transcriptomes, to highlight the interdependence of genomics and transcriptomics. Further, transcriptomes of moso bamboo have been compared under various developmental stages such as flowering (Cheng, Hou, et al., 2018), spatial fast growth of shoots (Li, Cheng, et al., 2018) and newly elongated shoots, as well as under experimental conditions such as auxin treatment and exposure to abiotic stress. A compilation of the outcomes of these studies is given in Table 4. Raw sequences of moso bamboo transcriptomes are publicly available in Sequence Read Archive database at the National Center for Biotechnology Information (www.ncbi.nlm.nih.gov/sra), European Molecular Biology

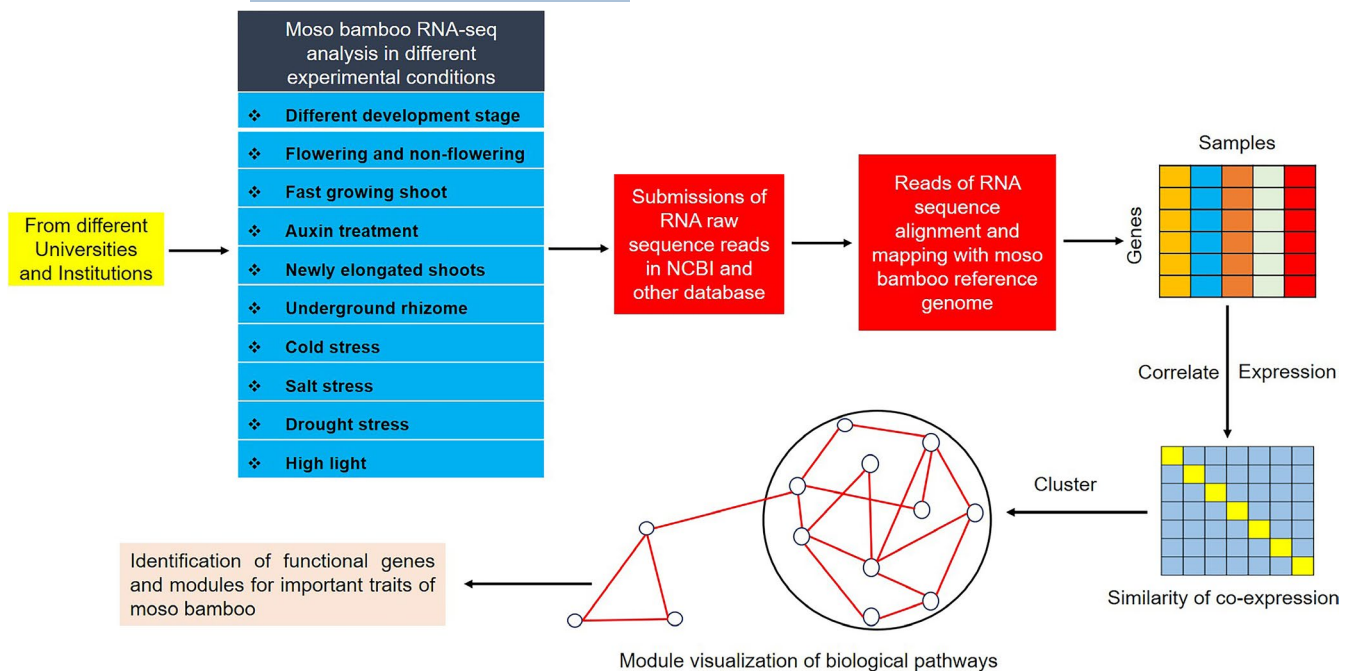


FIGURE 2 A flow model indicating a cooperative transcriptome analysis network for gene discovery in moso bamboo using publicly available datasets. The source of transcriptomes for different experimental conditions will be deposited in Sequence Read Archive database at the National Center for Biotechnology Information, European Molecular Biology Laboratory, and in the GigaScience and BambooNET databases, etc., by the partner institutions, which will then be added into the gene discovery pipeline involving comparative transcriptomics, coexpression networks, and validation

Laboratory, and in the BambooNET and GigaScience (<http://gigadb.org/>) databases. Recent transcriptome studies in moso bamboo illustrate the roles of endogenous hormones in culm development and identified many biological pathways related to cell wall biosynthesis, the flowering process, the shoot fast growth, and their role under abiotic stress (Cheng, Hou, et al., 2018; Li, Shi, et al., 2018; Wang et al., 2018). A coexpression network was established for flower development, and TFs, transposable elements, and noncoding RNA profiles were identified. The expression of the transcript was validated by quantitative real-time (qRT-PCR) analysis. Fan et al. (2013) recommended *TIP41* and *NTB* as reference genes for the reliable quantification of candidate gene expressions for moso bamboo. In a latest transcriptomic investigation, Liu, Wu, et al. (2020) had elucidated differentially expressed genes (DEGs) on cold response in moso bamboo, identifying more late-responsive genes than early-responsive ones under cold exposure. As many as 222 TFs belonging to 24 families and several C-repeat/dehydration-responsive element-binding factor (CBF) elements were found up-regulated under cold stress implying the presence of a complex cold response network in moso bamboo.

Proteomes are genome-wide translation products following gene expression. Understanding the proteome pattern of the plant response to developmental impulse can help in identifying the pathway through which the traits are expressed. Owing to this potential, proteomics studies are widely used

in understanding physiological response to various environmental conditions, be it a stress or a favorable condition. Such studies are being routinely used in commercial crops of the grass family Poaceae. Compared with other grass genomes, however, limited proteomic information is available in moso bamboo. Cui, He, Zhang, Duan, and Zeng (2012) investigated protein expression patterns in rapidly growing moso bamboo culms through two-dimensional electrophoresis (2-DE) and mass spectrometry (MS). By observing the internode elongation at different stages of moso bamboo development, a total of 258 spots showed differential expression, of which 213 were identified by matrix-assisted laser desorption/ionization time-of-flight (MALDI-TOF/TOF) mass spectrometry. These proteins were involved in different pathways, such as cell division, cell expansion, carbohydrate metabolism, protein synthesis, redox homeostasis, and amino acid metabolism. Internode- and stage-specific protein profiles were also identified. Proteins involved in culm development were highly expressed during cell division. Four endogenous hormones, indole acetic acid, gibberellic acid, abscisic acid, and zeatin riboside, strongly regulated the cell elongation phase. To improve bamboo proteomic studies, Yu et al. (2019) established an efficient method for total protein extraction in moso bamboo and mass spectrometry-based proteomics for gene annotation. The method predicted 10,376 coding genes and 1,015 long noncoding RNAs (lncRNA), providing a basis for proteomics-assisted genome annotation in moso bamboo.

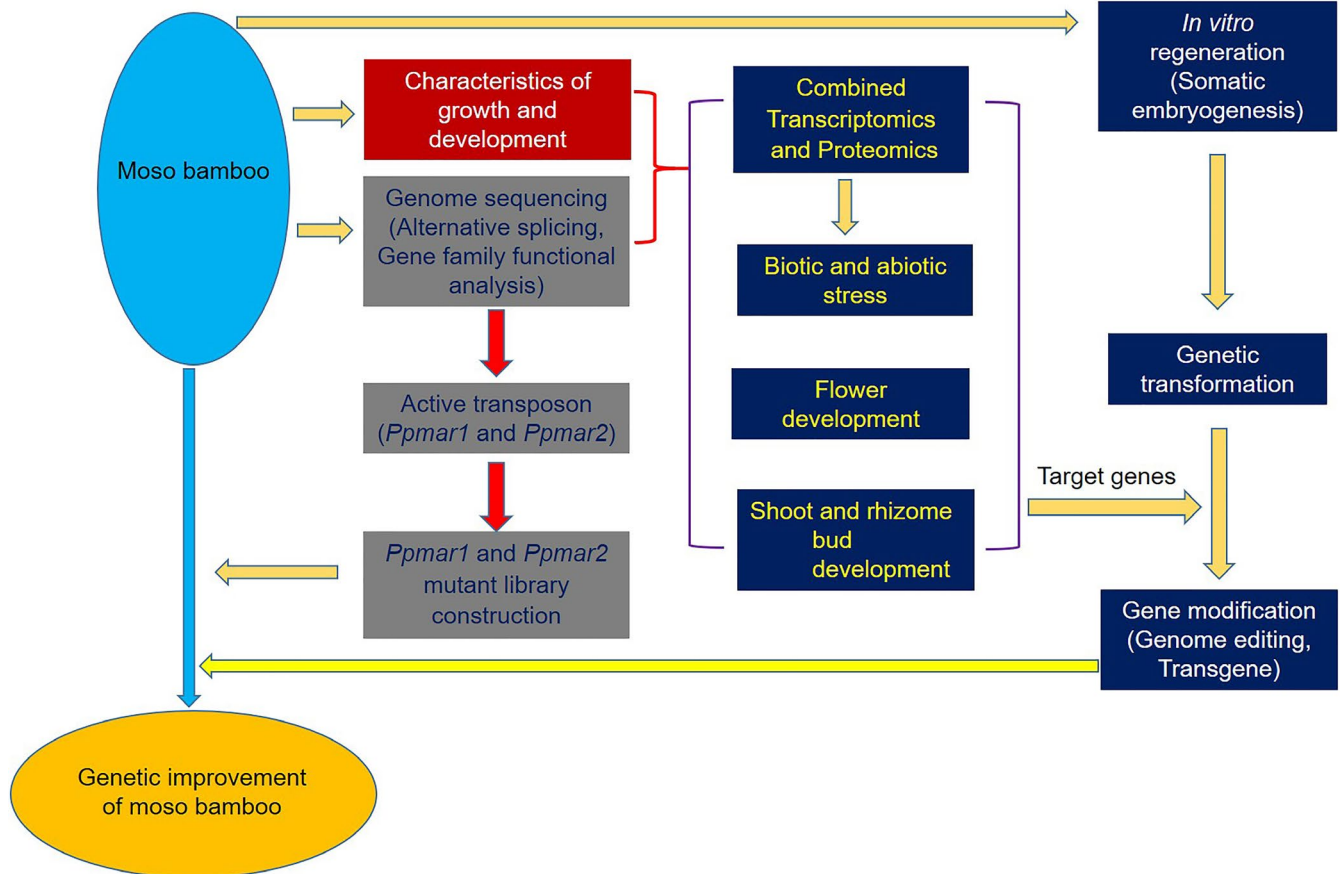


FIGURE 3 A schematic representation of different moso bamboo research areas using different biotechnology tools for genetic development of moso bamboo. White letters indicate the future direction of moso bamboo research

5.5 | Fast-growth internodes, floral development, and flowering time

One of the most intriguing features of bamboo biology, as seen in the case of moso bamboo, is the fast-growing nature of internodes. Although genetic connotations of this unique phenomenon are hardly understood, it has invoked great curiosity in the bamboo scientific community. Nevertheless, several genes such as TFs, plant hormones, cell cycle regulation genes, and genes involved in cell wall metabolism and cell morphogenesis have been implicated to play a crucial role in the rapid growth of moso bamboo shoots (Li, Cheng, et al., 2018; Peng, Zhang, et al., 2013). Very recently, acid invertases (*INVs*) have been found highly enriched in fast-growing internodes of moso bamboo and are believed to have a significant role to play in their accelerated growth (Guo, Chen, et al., 2020). *INV* genes such as *PhCWINV1*, *PhCWINV4*, and *PhCWINV7* have been demonstrated to increase biomass production when overexpressed in *Arabidopsis*. Similarly, increased accumulation of brassinosteroids (BRs) has also been observed in the fast-growing moso bamboo internodes. But, the role of BRs is still not well understood in abetting the fast growth, because when the gene *PSBRI* encoding for a mitochondrial localized protein was overexpressed in

Arabidopsis, BRs were seen negatively regulating the gene resulting in inhibited plant growth (Guo, Zhang, et al., 2020). The above findings throw light on the complex nature of molecular regulation of mechanisms in fast-growth internodes of moso bamboo.

As previously mentioned, flowering in bamboo is a peculiar phenomenon due to its long vegetative phase. Extending more than 60 years to bloom, with monocarpic nature wherein the seed production occurs only once in lifetime at the terminal phase, the trigger to flowering in moso bamboo still remains a puzzle. Therefore, the switch from the vegetative phase to reproductive stage is difficult to predict (Clark et al., 2015). Strong biochemical signaling is envisaged in the flowering process, because in general, all the shoots, both young and old, formed from a common rhizome flower together. Although previous studies have identified the importance of the mediacy meristem in shoot growth, understanding has remained limited of the nature of bamboo growth, infrequent sexual reproduction pattern, and long flowering intervals (Lee & Chin, 1960; Lin, He, Hu, Kuang, & Ceulemans, 2002).

Under the circumstances of no concrete information on the factors that trigger flowering in bamboos, the future genomic studies may drive inroads into unraveling its mystery. Analysis of coexpression networks from related grass

TABLE 4 List of transcriptome studies in moso bamboo under different experimental conditions, and their results including accession number

Phenology	Types of tissue	Sequencing technology	Types of assembly	Total number of genes identified
Different development stage	Culms of different internode	Paired-end reads (Illumina HiSeq TM 2000)	De novo	60,393
Flowering	Young leaves, rhizomes, roots, panicle 1 and 2, and shoot tips (20 and 50 cm)	Paired-end reads (Illumina HiSeq TM 2000)	De novo	31,987
Fast-growing shoot	Six different heights of the shoot (10, 50, 100, 300, 600, and 900 cm) and culms	Paired-end reads (Illumina HiSeq TM 2000)	De novo and the reference genome	16,519
Flowering and nonflowering	Leaf and panicle of flower	Paired-end reads (Illumina HiSeq TM 2000)	Reference genome	30,640,507 and 30,868,269
In vitro -derived reproductive and vegetative materials	Roots, shoots, and flowers	Roche 454 GS FLX Titanium, Illumina and 454 + Illumina (Hybrid)	De novo	11,646 for 454 datasets, 39,261 for Illumina dataset and 7,141 for the hybrid dataset
Fast-growing shoots at eight different heights (50, 100, 300, 600, 900, and 1,200 cm)	Culm tissue after leaf expansion	Paired-end reads (Illumina HiSeq TM 2000)	Reference genome	5,740 (isoforms)
Development stage	Leaf, rhizome, root, shoot, and panicle	Paired-end reads (Illumina HiSeq TM 2000)	De novo and the reference genome	3,038 (DEGs)
High light (1,200 $\mu\text{mol m}^{-2} \text{s}^{-1}$)	Leaves	Paired-end reads (Illumina HiSeq TM 2000)	Reference genome	19,059
Underground shoot (the wild-type (WT) and the thick wall variant)	shoots at the S-2 stage	Paired-end reads (Illumina HiSeq TM 2500)	Reference genome	1,050 (DEGs)
Auxin treatment	Root parts from 1-month-old seedlings	Paired-end reads (Illumina HiSeq TM 2500)	Reference genome	2,279 (DEGs)
Newly elongated shoots	Young shoots (approximately 25 cm above ground height)	Paired-end reads (Illumina HiSeq TM 2000)	Reference genome	27,254
Underground rhizome	Underground rhizome tip, lateral bud on the rhizome, new shoot tip, root initiated from the rhizome, and leaf	PacBio RSII sequencing system, Paired-end reads (Illumina HiSeq TM 2500)	Reference genome	11,902

Major findings	Accession number	References
The role of the endogenous hormone in culm development. Genes involved in signal transduction, translation, transport, and several metabolism pathways were identified. The microRNA expression profile was developed. Culm development is regulated by transcriptome, post-transcriptome, miRNA, and proteome	SRX329521	He et al., 2013
The first draft genome of moso bamboo revealing transposable elements, protein-coding genes involved in cell wall biosynthesis, flowering process, tRNA, rRNA, small nucleolar RNA, small nuclear RNA, miRNA genes	ERP001341, (EMBL)	Peng, Lu, et al., 2013
The candidate genes identified associated with the TFs, cell cycle regulation, plant hormones, cell morphogenesis, and cell wall metabolism during fast growth of moso bamboo shoots	SRP029431	Peng, Zhang, et al., 2013
The gene expression between flowering and nonflowering tissues and correlation of drought response genes during flower development. Various TFs of floral development, genes involved in flower development, and flowering time control were identified	SRR1187864, SRR1185317	Gao et al., 2014
Combination of Roche 454 GS FLX titanium and Illumina sequencing resulted in longer sequence lengths and complete transcriptome assembly. Identified 16 <i>BeMADS</i> genes and their expression levels were studied using qRT-PCR. Most of the <i>BeMADS</i> genes were up-regulated in flower tissue, and the expression pattern was similar to that of the rice genes	SRP043102	Shih et al., 2014
Investigation of the functions of AS events and isoforms in the physiological process during shoot growth. A comprehensive view of alternative splicing profiles to understand moso bamboo growth and development. Isoform expression showed that moso bamboo has four stages in the shoot growth	NA	Li et al., 2016
The transcriptional expression profile for plant growth and development. Gene structure and conserved motifs of GRAS TFs were identified. DEGs of panicle and leaf were higher in glutathione, photosynthesis, porphyrin, and chlorophyll metabolism	SRX082501-4, 7-12, SRR2035263, and SRR2035327	Zhao, Dong, et al., 2016
The response to high light conditions identifying global gene expression patterns, and annotation of LHC protein, LHC-like protein, and PsbS and pathways of ROS. Eight different families of TFs related to photosynthetic regulations were identified	SRR2035212, SRR2035263, and SRR2035327	Zhao, Lou, et al., 2016
The molecular mechanism of the thick wall variant and wild-type (WT). The candidate genes for cell wall synthesis, hormone metabolism, and TFs (bHLH, bZIP and MYB families) were identified. Gene expression in thick wall variant was higher than WT	SRP075216	Wei et al., 2017
The effect of exogenous auxin on crown and primary roots. Genes involved in auxin activity, such as auxin synthesis, auxin transport, and auxin signaling pathways are conserved in rice, bamboo, and <i>Arabidopsis</i> species. The conserved genes regulate the auxin pathway in moso bamboo	GSE100172	Wang, Gu, et al., 2017
The spatial regulation of hormones and the role of the transcriptome during the initiation of shoot growth. Growth hormones accumulated in the shoot apex and stress hormones were mainly found in the lower part of the shoot. Transcripts associated with cell wall metabolism, biosynthesis of phenylpropanoid metabolites, DNA synthesis, etc., were identified	PRJNA342231 (BioProject).	Gamuyao et al., 2017
Compared PacBio and Illumina reads. The post-transcriptional mechanism in the underground rhizome–root system was studied. Alternative splicing profile identified, which was enriched in post-translational protein modification, cellular carbohydrate metabolic process, and microtubule-based process	GSE90517	Wang, Wang, et al., 2017

(Continues)



TABLE 4 (Continued)

Phenology	Types of tissue	Sequencing technology	Types of assembly	Total number of genes identified
Different growth stages	Apical, middle, and basal parts of the bamboo shoot	Illumina GA-II	Reference genome	14,902
Fast-growing shoot	Seven different heights of shoot tips (50, 100, 300, 600, 900 and 120 cm) and culms	Paired-end reads (Illumina HiSeq™ 2000)	Reference genome	10,344 (DEGs)
Seedlings were treated with H ₂ O or GA ₃ (100 µM) for 4 hr.	Four-week-old seedlings	Paired-end reads (Illumina HiSeq™ 2500)	Reference genome	5,148 (DEGs)
Different developmental stages	Rhizome, root, shoot, leaf, sheath, and bud, during different developmental stages	Paired-end reads (Illumina HiSeq™ 4000) and PacBio sequencing platforms	Reference genome	25,225
Different development stages	Rhizome, roots, shoots, leaves, sheaths, and buds	Paired-end reads (Illumina HiSeq™ 4000) and PacBio sequencing platforms	Reference genome	63 <i>PeAQPs</i> , 22 <i>PePIPs</i> , 20 <i>PeTIPs</i> , 17 <i>PeNIPs</i> , and 4 <i>PeSIPs</i>
Elongated internodes (Wild-type and dwarf shengyin bamboo)	Young shoots from boosting stage	Paired-end reads (Illumina HiSeq™ 2000)	Reference genome	5,067 (DEGs)
Different growth stage	Shoot and mature culms	101-nt paired-end reads (Illumina HiSeq™ 2500)	Reference genome	29,731 (alternative splicing events)
Different flowering developmental stages and seedlings under cold, salt and drought stresses	Leaves and flowers	Paired-end reads (Illumina HiSeq™ 2000)	Reference genome	26 <i>PheDof</i>
Three-week-old seedlings treated at −2°C for different lengths of time	Leaves	Paired-end reads (Illumina HiSeq™ 2000)	Reference genome	2,463 (DEGs) and 222 (TFs)

Note: DEGs, differentially expressed genes; EMBL, European Molecular Biology Laboratory; GA₃, gibberellins; cis-NATs, cis-nature antisense transcripts; ROS, genes related to reactive oxygen species in bamboo; LHC, light-harvesting chlorophyll a/b binding; TFs, transcription factors.

species such as maize, rice, wheat, and barley may be one of the routes that may lead to the understanding of bamboo flowering. Yet, a limited number of genes related to flower development have been characterized in bamboo that belongs to from the MADS-box gene family (Biswas, Chakraborty, Dutta, Pal, & Das, 2016; Wysocki, Ruiz-Sanchez, Yin, & Duvall, 2016). In moso bamboo, sixteen *BeMADS* genes were identified, and most of them showed higher expression during flower development (Shih et al., 2014). In addition, forty-two *PeMADS* genes were reported and ectopic over-expression of *PeMADS5* in *Arabidopsis* was found to cause

early flowering and developed aberrant flower phenotypes (Zhang, Tang, et al., 2018). RNA-seq analyses during four important flower development stages in moso bamboo had led to the identification of candidate genes related to floral transition and flower development (Gao et al., 2014). The important genes included those belonging to DNA binding with one finger (Dof) and MADS-box family. Many differentially expressed microRNAs and their target genes participate in diverse primary biological pathways and play significant regulatory roles in moso bamboo flowering (Gao et al., 2015). More recent studies on the regulatory pathways

Major findings	Accession number	References
Key genes involved in secondary cell wall formation, lignin synthesis, cellulose, xylan, and NAC-MYB-based TFs were identified. Lignification was higher in the mature, middle, and basal segments	PRJNA392761	Zhang, Ying, et al., 2018
Cell division and cell elongation-regulated shoot growth. The hormone signaling (IAA, GA ₃ , BR, ZR, and ABA) genes regulated the shoot growth and dynamic changes in shoot anatomy. Cell cycle-associated gene expression was higher in early growth than in the slow growth of shoot. Coexpression network hormone signaling genes were observed	NA	Li, Cheng, et al., 2018
The roles of exogenous gibberellins (GA) in internode growth and lignin condensation. Identification of 932 cis-NATs, alternative splicing genes and GA altered post-transcriptional regulation that affected the regulation of photosynthesis in the development of seedlings by adjusting the carbon cycle	GSE104596	Zhang, Wang, et al., 2018
Updating of moso bamboo genome, improvement of the reference genome, and chromosome-level de novo genome assembly. The evolutionary view of alternative splicing and identification of alternative splicing genes and transposable elements. These genes are conserved	SRX2408703-28 and SRR7032261-69	Zhao, Gao, et al., 2018
Aquaporin (AQPs) functions studied in water transport in moso bamboo growth and development. A total of 63 <i>PeAQPs</i> genes were found, and all these were differentially expressed in different tissues. Circadian rhythm changes were positive at night and negative in the daytime shown by root pressure. Coexpression network of <i>PeAQPs</i> and sugar transport genes	SRX2408703-SRX2408728	Sun et al., 2018
Genes involved in regulating mechanism for internode growth were identified. Genes for cellulose and lignin biosynthesis pathways, hormone biosynthesis, and signal transduction were significantly expressed in the internodes of wild and shengyin bamboo. Cell wall expansion, phytohormone signaling control, and phytohormone signaling were shown	SRP133731	Wang et al., 2018
The alternative splicing mechanism in transcriptomes was studied. Genes (36.17%) undergo alternative splicing, which was associated with gene characteristics and gene expression. Alternative splicing was enriched in dominant splice sites and varied in different tissue	SRR961047, SRR1187864, and SRR1185317	Li, Shi, et al., 2018
Identification of 26 <i>PheDof</i> TFs genes classified into five groups based on expression during flowering. The coexpression network showed <i>PheDof12</i> , <i>PheDof14</i> , and <i>PheDof16</i> were associated with flower development	NA	Cheng, Hou, et al., 2018
Genes and TFs from different families were mostly differentially expressed at 24-hr cold treatment. Cold response genes in moso bamboo are late-responsive. Phytohormone-related pathways played important roles in cold-stress response		Liu, Wu, et al., 2020

of flowering behavior in moso bamboo revealed that genes such as *PheDof1*, *PheMADS14*, and six microRNAs were critical in these pathways (Ge et al., 2017). Further, molecular mechanisms governing moso bamboo flowering and growth control have very recently been elucidated (Yang, Chen, et al., 2019; Zhang, Tang, et al., 2018). Furthermore, Liu, Cheng, Xie, Li, and Gao (2019) observed that *PheDof* was highly expressed in bamboo leaves during flowering, the activity of which declines during flower development. Overexpression of *PheDof* in *Arabidopsis* was reported to cause early flowering (Liu et al., 2019). Similarly, high expression of two

miRNAs, *miRNA159* and *miRNA166*, was observed in stamens, with concomitant down-regulation of their target TFs, *PheMYB98* and *PheMYB42*. *Phe-miR159* overexpression affected anther wall thickening in *Arabidopsis* by inhibiting its target, *AtMYB33* TF (Cheng, Hou, et al., 2019).

5.6 | Tolerance to abiotic stress

Unlike other cereal crops, external stress factors that affect bamboo productivity are mainly abiotic stresses. Although

TABLE 5 In vitro regeneration of moso bamboo through organogenesis and somatic embryogenesis using different explants

Regeneration method	Explant	Basal medium	PGRs used for induction of shoot initiation, callus, and somatic embryo	PGRs used for regeneration of shoot, root, and in vitro flowering	Main results	References
Organogenesis	Zygotic embryo	White major and minor elements	Nil	Nil	Shoot formation	Alexander & Rao, 1968
	Nodal segments	MS	Nil	## TDZ (0.1 mg/L); # TDZ (0.01 mg/L) + 2,4-D (0.5 mg/L); *** TDZ (0.01 mg/L)	Shoot regeneration and in vitro flowering	Lin & Chang, 1998
	Inflorescence	MS	Nil	## TDZ (0.1 mg/L); # NAA (5.0 mg/L)	Inflorescence proliferation	Lin, Vidmar, & Chang, 2004
	Inflorescence	MS	Nil	## 2,4-D (1 mg/L); # NAA (10 mg/L); *** NAA (5 mg/L) + ACC (1 mg/L)	Shoot regeneration, reflowering, and postflowering	Lin et al., 2005
	Segments of in vitro spikelets	MS	* TDZ (0.455 μ M) + 2,4-D (13.57 μ M); ** Kinetin (9.3 μ M) + 2,4-D (13.57 μ M)	*** TDZ (0.5 μ M) + sucrose (30 g^{-1}); # NAA (53.8 μ M)	In vitro flowering and plantlet survival	Lin, Lin, & Chang, 2003
Somatic embryogenesis	Nodal and internodal segments	MS	* Kinetin (9.2 μ M) + 2,4-D (13.6 μ M) + 0.1% (v/v) coconut milk + 6% (w/v) sucrose; ** 2,4-D (13.6 μ M) + TDZ (0.046 μ M) + 3% (w/v) sucrose;	## TDZ (0.455 μ M)	In vitro regeneration	Lin, Lin, & Chang, 2004
	Zygotic seed embryos	MS	* 2,4-D (4.0 mg/L) + Zeatin (0.1 mg/L); ** 2,4-D (4.0 mg/L)	## Zeatin (7.0 mg/L); # NAA (2.0 mg/L)	In vitro regeneration	Yuan et al., 2013

Note: PGRs: plant growth regulators; MS: Murashige–Skoog medium; TDZ: thidiazuron; 2,4-D, 2,4-dichlorophenoxyacetic acid; NAA: 1-naphthaleneacetic acid; ACC: aminocyclopropane-1-carboxylic acid; *: Callus initiation; **: somatic embryo formation; ***: in vitro flowering; ****: plant regeneration and in vitro flowering; #: rooting; ##: plant regeneration.

more than 1,200 pests are recorded on bamboos, most of them are minor in nature except for few isolated infestations that were serious in nature. Notwithstanding, bamboos have a wide environmental adaptation profile, ranging from tropical to temperate and montane ecology to plains, their mechanisms to cope with environmental stress are contrastive. Owing to their perennial nature, bamboos encounter stress factors such as cold, drought, salinity, and high temperature more commonly than any other grass species. Accordingly, abiotic stress tolerance is key to the sustainability of bamboo as a natural species and an industrial crop although the underlying molecular mechanisms are still not completely understood.

One of the major abiotic factors that adversely affect bamboos is drought. In moso bamboo, drought is found to influence transpiration, warranting a specialized water use strategy to cope with the adverse consequences (Gu et al., 2019). In moso bamboo, analyzing the dehydration-responsive element-binding (DREB) genes, *PeDREB2A* and *PeDREB1A*, Wu, Li, et al. (2015) have found that these genes differentially expressed in leaves and roots when challenged with stress factors such as cold, drought, and salt stress. DREB proteins are TFs known to play a crucial role in abiotic stress response, particularly to drought and salt, by binding to drought-responsive elements (DREs) and regulate the reporter gene expression (Liu, Zhao, Yamaguchi-Shinozaki, & Shinozaki, 2000). Adding to this, Huang, Zhong, et al. (2016) identified a total of 23 genes encoding for the late embryogenesis abundant (LEA) proteins in moso bamboo, where approximately 78% of *PeLEAs* were up-regulated under dehydration and cold stresses. Furthermore, 50% of *PeTIFY* genes were reported to get up-regulated during dehydration and cold stresses (Huang, Jin, et al., 2016). The role of aquaporin (AQPs) genes in regulating water balance and nutrient acquisition has been demonstrated in moso bamboo (Sun, Li, Lou, Zhao, & Gao, 2016). In total, 26 AQP genes falling into four different groups have been identified, which shared considerable homology to rice AQP genes. Increased AQP expression under water and salt stress could be observed through qRT-PCR analysis in moso bamboo tissues. Proteins belonging to calmodulin (CaM)/CaM-like (CML) having an isoleucine (I)-glutamine (Q) domain (IQD)-binding motif are coded by *IQD* genes that are known to regulate plant defense mechanisms. In moso bamboo, 29 nonredundant *PeIQD* encoding genes were identified and *PeIQD* gene expression showed a 12-fold increase under drought and methyl jasmonate treatments (Wu et al., 2016). Besides, a UDP-galactose-4-epimerase (UGE) gene from moso bamboo *PeUGE* when overexpressed in *Arabidopsis* improved salinity and drought tolerance by increasing lateral roots (Sun, Li, Lou, Zhao, Yang, et al., 2016). UGE is a key enzyme in

the galactose metabolism and is believed to play an important role in cell wall synthesis under stresses. Zeaxanthin epoxidase (ZEP), an important protein for plant response against different environmental stresses, has been investigated by overexpressing the moso bamboo gene, *PeZEP* in *Arabidopsis*. The transgenics showed enhanced tolerance to drought (Lou, Sun, Li, Zhao, & Gao, 2017) and was found up-regulated under high light ($1,200 \text{ mmol m}^{-2} \text{ s}^{-1}$) and high temperature (42°C), whereas, when exposed to low temperature (4°C) and exogenous ABA treatment, *PeZEP* was down-regulated, implying that *PeZEP* inevitably plays a major role in response to high temperature and drought. Based on expression profile and phylogenetic analysis, Wu et al. (2018) isolated a drought stress-related candidate gene *PeDi19-4* from moso bamboo. *PeDi19-4* overexpression in rice and *Arabidopsis* enhanced their drought and salt tolerance levels and increased the sensitivity to ABA during seed germination and growth. WRKY genes have multiple biological functions in plant systems. Overexpression of moso bamboo's *PeWRKY83* gene in *Arabidopsis* accumulated more endogenous ABA under salt stress conditions and regulated stress-induced ABA synthesis (Wu et al., 2017). Very recently, Liu, Gao, et al. (2020) reported that *PeTCP10* conferred drought tolerance of transgenic and directly targeted the stress-/ABA-responsive gene BT2. This indicated that moso bamboo counters drought and salt stresses via the ABA-dependent signaling pathway. Zhao et al. (2019) described that expression of *PhePEBP* family genes, especially *PheFT9*, *PheTFL2*, and *PheTFL8*, involved in the activation of dormant buds and seedling growth is regulated by plant hormones and drought stress.

Additional genes that contribute to drought tolerance in moso bamboo include amino acid/auxin permease (AAP) and VQ genes. AAP genes underwent a duplication event roughly 12 Mya ago, and potentially contribute to the adaptation of moso bamboo to drought, salt, and cold stress (Liu et al., 2017). Wang, Liu, et al. (2017) found by genome-wide analysis that moso bamboo possess 29 VQ genes and revealed that *PeVQ* genes showed different expression patterns in different tissues or developmental stages under abscisic acid, polyethylene glycol, and salicylic treatments. Most recently, the same group further identified the interaction of *PeVQ28* gene with *PeWRKY83* TF in the yeast nucleus (Cheng et al., 2020). Their results suggest that the genes related to abiotic stress underwent a large-scale evolutionary event, between 12 and 40 Mya in moso bamboo, rice, and other cereals. As mentioned earlier, moso bamboo has an elaborate adaptation mechanism to counter stress effects and to alter phenotypic features accordingly. The details of the network of genes involved in stress response and their relationship to growth and flowering need to be explored further.

6 | TRANSGENIC APPROACHES TO CROP IMPROVEMENT

6.1 | Plant regeneration and clonal propagation

Conventionally bamboos are propagated through clonal propagation, such as rhizome and culm cuttings, as well as by clump division. Seed propagation is also practiced but is very limited due to nonavailability of sufficient seeds for mass production. Moreover, conventional propagation requires large nurseries and infrastructure that needs high investment costs. Therefore, the most viable alternative is micropropagation through in vitro culture (Nadgauda, Parasharami, & Mascarenhas, 1990). The first successful report on micropropagation of bamboo (*Bambusa* sp.) was described by Alexander and Rao (1968) using zygotic embryo explants. Since then, several attempts have been reported and found that different species and cultivars within species require different in vitro regeneration techniques (Mudoi et al., 2013). Besides, organogenesis potential also varied between different bamboo types and depended on the age of the explants used (Singh et al., 2013). Qiao et al. (2013) have established the regeneration platform in ma bamboo for anther culture, by which homozygous diploid bamboo plants can be obtained in one generation. Thus, the breeding time can be reduced, accelerating varietal improvement since bamboo's vegetative growth phase is too long. However, this method also varied between genotypes and developmental stage of immature pollen grain/ microspores (Niazian & Shariatpanahi, 2020). Due to this varying clonal requirement, development of a common protocol for large-scale and efficient in vitro regeneration has been a major bottleneck in micropropagation of bamboo (Ye et al., 2017).

In spite of such drawbacks, successful plant regeneration through somatic embryogenesis and indirect organogenesis has been established for moso bamboo (Table 5). Nodal segments and inflorescences are generally used as explants for organogenesis (Lin & Chang, 1998; Lin, Lin, & Chang, 2005). Plant growth regulators (PGRs) such as thidiazuron (TDZ), 2,4-dichlorophenoxyacetic acid (2,4-D), 1-aminocyclopropane-1-carboxylic acid (ACC), and 1-naphthaleneacetic acid (NAA) are reported suitable for shoot regeneration, in vitro flowering, and rooting. For somatic embryo induction, in vitro spikelets, nodal segments and zygotic seed embryos are used together with TDZ, 2,4-D, kinetin, zeatin, and coconut milk as PGRs. TDZ is the hormone of choice for somatic embryo regeneration and in vitro flowering while NAA is the best used for rooting. Micropropagation techniques are now being used commercially in bamboo propagation. In moso bamboo, in vitro flowering has been demonstrated to shorten breeding time (Lin & Chang, 1998). Tissue culture systems have also been used to generate a cDNA library of the multiple shoots grown in vitro, which could be used to study of

the genes involved in shoot development, photosynthesis, and metabolism (Liu, Wu, Tsay, Chang, & Lin, 2008).

6.2 | Genetic transformation and gene editing

An efficient tissue regeneration system is the first step for successful transgene incorporation and genetic transformation. In addition, genetic fidelity of the regenerants is highly desirable, for ensuring efficiency of the regeneration and transgene expression. In bamboo, in spite of the use of several plant tissues as the explant source, as well as varying cultural requirements, occurrence of somaclonal variants is seldom reported. Several attempts have been reported previously on bamboo genetic transformation in species such as *D. latiflorus* (ma bamboo), *D. hamiltonii*, and *D. farinosus* (Jiang & Zhou, 2014; Qiao et al., 2014; Sood et al., 2014). In particular, Qiao et al. (2014) have successfully established a genetic transformation system in ma bamboo using anther culture that was employed for transferring a bacterial gene, *CodA*, encoding for choline oxidase to impart cold tolerance into bamboo genome. Although *Agrobacterium*-mediated transformation and particle bombardment have been used in bamboo, the transformation frequency was reported limited (Sood et al., 2014). These studies have set the foundation for future research wherein actual crop improvement through genetic transformation in bamboos has been envisaged. Recently, Ye et al. (2017) developed a successful *Agrobacterium* transformation protocol for ma bamboo, a hexaploid species, by taking 8 months to get healthy calluses, and 7–8 months for the transformation. As far as the current information goes, the reports of improvement of agronomic traits in bamboo through genetic engineering remain limited only to one species, ma bamboo. Low efficiency and slow regeneration are major limitations for successful transformation in bamboo.

Latest advancements in gene editing technologies have found increasing use of clustered regularly interspaced short palindromic repeat (CRISPR)–CRISPR-associated endonuclease (Cas9) system in several crop species (Doudna & Charpentier, 2014). Very recently, Ye, Chen, et al. (2019) established a CRISPR/Cas9 system in ma bamboo by targeting all homo-alleles or specifically one allele of a gene. Using this technology, they could demonstrate the plant height changes by knocking out one gibberellin-responsive gene in ma bamboo.

To the best of our knowledge, no report is available either on the successful genetic transformation or on gene editing in moso bamboo, although plantlet regeneration via embryoid germination through callus induction in moso bamboo has been demonstrated (Yuan, Yue, Wu, & Gu, 2013).

A while back, no further advancements have been achieved with respect to transgenic development. Now, the recent release of the moso bamboo genome is expected to boost the attempts on gene editing and genetic transformation in moso bamboo using the abovementioned methods. However, a concerted effort is required to study the molecular mechanism of somatic embryogenesis and regeneration for achieving a successful transformation system to reap the benefits of gene editing.

7 | FUTURE DEVELOPMENT OF THE BAMBOO INDUSTRY TO IMPROVE FOOD AND ENERGY SECURITY

In a recent review on the global bamboo industry, Zhaohua and Wei (2018) reported about the underutilized bamboo forests in several countries. This is because the industrial approach with bamboo as the prime resource has not been comprehensively developed in these nations, except for the traditional use for immediate human needs. Based on the concept of circular economy, that stands to minimize the inputs and the waste to improve the efficiency of a production system, the bamboo industry requires an approach that combines considerations of human needs with that of larger industrial uses in an economically sustainable fashion (Korhonen, Honkasalo, & Seppälä, 2018). Toward developing sustainable goals for bamboo industrialization, several international organizations (Table S1) play key roles toward scientific research, industry development, and trading systems (Zhaohua & Wei, 2018) and use several databases in this process.

The development of bamboo industry in China perhaps supersedes similar development anywhere else in the world. In China, bamboo industry has grown way beyond the conventional, developing newer products that find unconventional applications, such as underground pressure pipelines, utility tunnels, high-speed train carriages, containers, large-scale storage tanks, and disaster resistant houses (Zhaohua & Wei, 2018). Taking advantage of high axial tensile strength and flexibility of fiber (Ghosh, Chaudhuri, Dey, & Pal, 2013), the bamboo winding composite is a biocomposite material built to make underground pressure pipes. Developed by Zhejiang Xinzhou Bamboo-Based Composites Technology Co., Ltd., this material is eulogized as the first-ever bamboo-based product in the underground delivery systems in the world. Made out of long bamboo slivers by reinforcing them in resin matrix and wound in a mechanical arch-shaped winder, winding composite is a lightweight alternative to glass fiber-reinforced polymer (GFRP). It has mechanical strength equivalent to GFRP, while being less dense by 46.1%–54.9% (Chen, Zhang, He, Zhang, & Yue, 2019). Economic potentials of such developments in China have

started reflecting as opportunities for the stakeholders in the industry. Recently, by cultivating bamboo shoots alone, a farmer household in the Lin'an District of Hangzhou City of the Zhejiang Province had reportedly earned one million US dollars $\text{ha}^{-1} \text{year}^{-1}$ (Zhaohua & Wei, 2018). Although such exceptional success stories exist, still, many stakeholders in the industry lack the necessary experience and knowledge to recognize the potential of the developing bamboo industry. Therefore, capacity building and knowledge dissemination among the stakeholders and building of new cross-disciplinary networks should be integrated as the indispensable goals for the bamboo industry development. Institutional support is also essential in developing bamboo-based industries as practiced in Yibin City of Sichuan Province in western China. Yibin is a historically important trading place located in the junction of Min and Yangtze, China's longest rivers. In 2018, a new campus of Sichuan University of Science and Engineering (www.suse.edu.cn) was established in Yibin to carry out extensive research on bamboo. To emphasize its role, the city is adorned with bamboos along with its roads and within the city area. Here, future bamboo research will be conducted in collaboration with Zhejiang A&F University, Hangzhou, Zhejiang (www.zafu.edu.cn), for the development of bamboo industry.

Key factors for the sustainable development of the bamboo industry are the characteristics of bamboo resources and their geographical distribution (Zhaohua & Wei, 2018). Conservation of bamboo germplasm and genotype improvement therefore are considered as key targets in the development programs (Figure 3). For the practical development of bamboo products at an industrial scale, an inclusive development model should consider product innovation, product structure optimization, capacity building, product demonstration, policies, and multistakeholder participation, besides ensuring the relentless flow of raw materials. Showcasing these developmental goals, the 9th China Bamboo Culture Festival opened in Meishan City, Sichuan Province, on 12 October 2019, identified its theme as *Promoting bamboo culture and developing bamboo industry* (www.ilikebamboo.com).

The genetic implications of the bamboo industry improvement should therefore be underlined with the characteristics of the bioresources for industrial applications. Among the fast-growing woody bamboos of the world, moso bamboo adorns a special position as one of the versatile species for industrial development. Several characteristic features channelize various species into separate industrial applications. These variations, accumulated along the evolutionary journey of the bamboos, need to be leveraged to engineer bamboo for specific needs. For instance, while most of the bamboos remain green throughout the growth stages, species such as *Phyllostachys vivax* cv. *aureocaulis* and *Pseudosasa japonica* cv. *akebonosuji* exhibit myriad of colors such as yellow,

green, purple, red, brown, and white at different growth stages on the culm and leaf (Xia et al., 2015; Yang et al., 2015). These species can, therefore, be recruited for ornamental industries, for which the genetics of color formation could be important information for future development. Similarly, species specificity of vascular bundle strength (Ahvenainen et al., 2017), lignin accumulation, and pith cavity formation (Guo, Sun, et al., 2019; Wang, Keplinger, Gierlinger, & Burgert, 2014) can be genetically manipulated at the cellular level with the critical understanding of the genomics of such traits. Therefore, genetic manipulation can bring in advantages for industrial applications resulting in various categories of products such as food, energy resources, biochemicals, construction materials, and household products.

8 | CHALLENGES, CAVEATS, AND BIOTECHNOLOGICAL OPPORTUNITIES TOWARD SUSTAINABLE DEVELOPMENT

Summarizing the challenges in moso bamboo improvement, in this final section, we would highlight the scientific and environmental caveats that potentially impede sustainable development. We further attempt to augment the biotechnological opportunities to address these threats.

The first and foremost challenge in moso bamboo improvement arises out of the slow pace of breeding, which is majorly associated with long flowering intervals and large population size. Further, asynchronous flowering may also pose additional challenges in hybridization. Biotechnological interventions could help in the induction of flowering in controlled conditions, particularly in *in situ* or *ex situ* gardens, so that natural recombination opportunities could be exploited in achieving additional variability. Toward achieving this, the development of germplasm resources is essentially required. The *in situ* conservation, nature reserve, and bamboo gardens may be useful in manipulating the breeding populations to aid the acceleration of the breeding programs.

Further, the genetics of monocarpic behavior could also help in fetching solutions to achieve accelerated breeding. Since the flowering is the terminal phase of the life cycle, asynchronous flowering poses a great challenge in hybridization. Although, moso bamboo exhibits fast-growth behavior, the understanding of the exact conditions under which the growth is regulated remains as the second major challenge. The critical factors that qualify moso bamboo as an industrial crop are its exceptionally fast growth, biomass turnover, lignin biosynthesis, and high mechanical strength of the wood. This information on the fast growth is essentially required to tame the bamboo as an industrial crop, because without which the quantum of bamboo production and the spatial requirement for the bamboo culture are difficult to manage.

No much-detailed genetic information is available about the expression of these traits. While fast growth and biomass regulate the supply of industrial raw materials, the mechanical strength and lignification decide the industrial quality of the bamboo in converting into value-added products. The bamboo quality is of particular importance in channelizing a sufficient quantity of bamboos into different quality segments suitable for specialized uses.

Although, the current knowledge of the whole-genome information can be leveraged for bamboo improvement, still much more remains unknown than the facts that are known about moso bamboo biology. This warrants more intensive basic research in addition to the applied ones, in order to achieve a scientific breakthrough in bamboo industrialization. However, technologies are now available to secure capacious gaps using transcriptomic, proteomic, and metabolomic routes to understand underlying biochemical pathways of the target traits for taking full advantage toward bamboo development. One such viable technology recently emerged is genome editing. Nevertheless, this technique is interdependent on the *in vitro* plant regeneration systems, which also uses genetic transformation systems to achieve the resultant transformants. Therefore, an efficient tissue regeneration system needs to be developed in moso bamboo for taking advantage of genetic transformation and the gene editing for the improvement. Current stride toward this goal is very minimal, and hence, this has to be considered as a formidable challenge in moso bamboo genetics.

Nanopore sequencing technology and CRISPR/Cas9 await applications in bamboo research. Further, a reliable anther culture system is yet to be developed in moso bamboo, which slows down the production of doubled haploid lines. Alternatively, as in related grass genomes, haploid inducer systems can also be explored in bamboo for the development of haploids. Induction of *in vitro* flowering could also be explored toward haploid development. An integrated approach combining the above techniques may drive the development of doubled haploids and the population development that speeds up the bamboo-breeding process.

As there is a conspicuous absence of a strong breeding system, breeding toward stress tolerance remains underdeveloped in moso bamboo. Bamboo cultivation is threatened by several adverse factors such as drought, salinity, nutrient deficiency, and land degradation. Currently, the natural tolerance is the only source available in combating these adverse factors. Recent interest on the industrial importance of bamboo has already mobilized large producers such as China to go into large-scale modes. Large-scale bamboo production will increase the threat of biotic and abiotic stresses in bamboo cultivation. Besides, the threat of climate change that is sporadically appearing in different geographical regions also may jeopardize bamboo development. Notwithstanding, many industrial uses of bamboo still await

discovery for refinement. For making such sustainable innovations, better cooperation between science and industry is mandatory that may be extended across regions around the bamboo world.

ACKNOWLEDGEMENTS

This work was funded by grants from the National Natural Science Foundation of China (grant nos 31870656 and 31470615) and the Zhejiang Provincial Natural Science Foundation of China (grant no. LZ19C160001). We sincerely thank Professor Qiang Wei, Co-Innovation Center for Sustainable Forestry in Southern China, Nanjing Forestry University, Nanjing, Jiangsu, China, for reviewing the manuscript, and we would like to extend our sincere gratitude and appreciation to all reviewers for their valuable comments.

CONFLICTS OF INTEREST

All the authors have declared no conflict of interest.

AUTHOR CONTRIBUTION

MR planned, designed, and wrote the review. MR, KY, KKV, and MZ outlined and edited the review. MR and AS wrote the stress development chapter. MR, KY, AS, KKV, MZ, CJ, and VS edited and revised the review.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Ramakrishnan M, Yrjälä K, Vinod KK, et al. Genetics and genomics of moso bamboo (*Phyllostachys edulis*): Current status, future challenges, and biotechnological opportunities toward a sustainable bamboo industry. *Food Energy Secur.* 2020;9:e229. <https://doi.org/10.1002/fes3.229>